Effects of Water Removal on a Hawaiian Stream Ecosystem[1]

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Abstract: A 3-year study of Wainiha River on Kaua'i, Hawai'i, was carried out to determine the impact that water removal had on key stream ecosystem parameters and functions. The study area included a diversion dam for a hydroelectric plant that removes water at an elevation of 213 m and returns it to the stream about 6 km downstream at an elevation of 30 m. There were two high-elevation sites, one with undiverted flow and one with reduced flow, and two low-elevation sites, one with reduced flow and one with full flow restored. Monthly samples were taken of instream and riparian invertebrates and plants. When samples from similar elevations were compared, dewatered sites had lower concentrations of benthic photosynthetic pigments than full-flow sites, and benthic ash-free dry mass (AFDM) was higher at the two low-elevation sites regardless of flow. Benthic chlorophyll *a* (chl *a*) and AFDM were higher in summer months than in the winter. Benthic invertebrate abundance was highest at the full-flow, low-elevation site and benthic invertebrate biomass was highest at the full-flow, high-elevation site. Season had only marginal effects on abundance and biomass of benthic invertebrates. Diversity of benthic invertebrates was higher at the more-downstream sites. Abundance of drifting invertebrates was highest at the site above the diversion dam and generally higher in winter than in summer months. Biomass of drifting invertebrates was also highest at the above-dam site but there was little seasonal difference. Almost all parameters measured were lowest at the site just downstream of the diversion dam. The biotic parameters responded only weakly to flows that had occurred up to 1 month before the measurements were made. Flow, elevation, and season interact in complex ways that impact ecosystem parameters and functions, but water diversion can override all these environmental factors.

In the history of limnology, the study of rivers (lotic systems) has lagged behind that of lakes (lentic systems). By the first decades of the twentieth century the basic understanding of the dynamics of thermal stratification provided a common framework for numerous subsequent studies of lentic systems (Ruttner 1953, Hutchinson 1957). For a long time students of rivers had no such unifying theme: hydrologists studied channel formation and, more practically, flood control, and biologists tended to focus on game fish or the production of food for these fish (see Hynes 1970 and Cummins et al. 1995 for historical accounts). Realization of the importance of complex interactions between the geomorphological setting of the stream and the physical and biological properties of the stream system set the stage for a conceptual model of stream dynamics based on func-

[1] This project was funded by the Dingell-Johnson/Wallop-Breaux Sport Fish Restoration Fund administered by the Hawai'i State Division of Aquatic Resources, Department of Land and Natural Resources. Manuscript accepted 29 December 2004.

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Pacific Science (2006), vol. 60, no. 1:1–47
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tional properties (Hynes 1975). Two features of lotic systems, the continuous nature of the stream system and the fact that upstream processes cumulatively impact downstream communities (Fisher 1983), were drawn together in the development of the "river continuum concept" (Vannote et al. 1980). The focus of this hypothesis was on expectations for a system of communities serially linked by factors controlled by the directional water movement (Newbold et al. 1982, Elwood et al. 1983). The river continuum concept made several testable predictions concerning changes in stream system parameters and biotic functions as water flows from high-elevation, low-order streams to lower-elevation, high-order streams. These predictions included a decrease in heterotrophy relative to autotrophy, a replacement of shredding invertebrates by filtering invertebrates, and an increase in fine suspended material relative to coarse suspended material. Although much refined and modified (Cummins et al. 1995), this concept still offers stream ecologists a unifying theme around which to develop theories and design hypotheses. Over the years the model and its components have been reviewed and revised (Winterbourn et al. 1981, Pringle et al. 1988, Mihuc 1997, Wright and Li 2002), but the river continuum concept still serves as a powerful organizing framework and a valuable source of hypotheses. In light of our study, it should be noted that in most formulations of the river continuum concept the independent variable is stream order, and as we discuss here, this metric may not be as meaningful in high-island tropical streams as in continental settings.

Stream ecological research, particularly in Europe and North America, has also seen major growth, with the emphasis in many important studies on higher levels of organization (Fontaine and Bartell 1983, Lampert and Sommer 1997), on how biotic interactions in streams relate to more general ecological thinking (Barnes and Minshall 1983), and on the increasing demand for water (Richter et al. 1997, Poff et al. 2003). Hildrew and Townsend (1987) described how, in the course of the development of these ideas, there has been a change in emphasis from thinking that river communities are controlled primarily by physical factors, to the view that biotic interactions are most influential, and then back to an intermediate position. Disturbance of river communities has been a central focus in this growth of lotic science, with much thought being given to how to define and quantify disturbance in systems that are inherently dynamic (Resh et al. 1988, Poff 1992, Richter et al. 1997, Bradt et al. 1999, Imbert and Perry 2000, McCabe and Gotelli 2000, Gjerløv et al. 2003). Disturbance can arise from many sources, but most attention has been devoted to disturbances resulting from changing flow conditions. These disturbances can arise as a function of the magnitude of flow in the channel (the drought/flood continuum), combined with the predictability/frequency of flow dynamics (Richter et al. 1996). Much effort has been devoted to trying to map ecological impacts of alterations in flow onto Connell's (1978) intermediate disturbance model (Ward and Stanford 1983, Reice 1985, Poff and Ward 1989). This focus on variability in flow and its effect on stream communities echoes more general ecological questions about the importance of variability per se as a critical environmental parameter (Benedetti-Cecchi 2003). The study of tropical streams, which has also seen substantial growth during the latter part of this period (Bright 1982, Angermeier and Karr 1983, Moyle and Senanayake 1983, Power 1983, Covich 1988, Lyons and Schneider 1990, Jackson and Sweeney 1995, Larned 2000, Larned et al. 2003), has further enriched the field of stream ecology.

Another research area that saw development in the past 30 years relates to what are termed regulated rivers. These are typically streams that have water development projects that divert or impound water for various purposes (Ward and Stanford 1979, 1995, Petts 1984, Craig and Kemper 1987, Gore and Petts 1989, Gleick 2003, Richter et al. 2003). This water can be released at the discretion of water managers, resulting in flow patterns quite unlike those seen in unmodified streams. Because the timing and volume of release are under direct control, rigorous tests of a range of hypotheses can be carried out in

regulated streams (Blinn et al. 1995). One outcome of this work is that water managers have come to realize that variation in flow can have detrimental effects at least as great as below-average flow (Poff and Ward 1989, Poff 1992, McCabe and Gotelli 2000).

In Hawai'i, beginning in the 1970s, there was an increase in research on freshwater ecology but with the primary emphasis directed at species and population levels. Much of this work dealt with the macrofauna, particularly the native amphidromous gobioid fishes, shrimps, and mollusks of Hawaiian streams (Kinzie 1990, Fitzsimons et al. 1993, Brasher 1997, Keith 2003, McDowall 2003). There was little attention given to the community and ecosystem levels of organization of streams in the state (Larned 2000, McIntosh et al. 2002). The identity (Vis et al. 1994, Sherwood 2004*a*) and production (LaPerriere 1995, Larned and Santos 2000, Sherwood 2004*b*) of the in-stream algae have received only limited attention. The smaller faunal elements, particularly the ubiquitous aquatic insects, are only recently becoming the focus of research (Kido et al. 1993, Polhemus and Asquith 1996, Benbow et al. 1997, Eldridge and Miller 1997, Kondratieff et al. 1997, Englund 2000, 2002, Englund et al. 2001).

Increasing demands for water in the state of Hawai'i have put tremendous pressure on water managers, who require a sound basis for making water allocation decisions (DAR 1996). Of particular concern in such decisions is the importance of naturally occurring variability in flows (Richter et al. 1996). Such variability might be an important aspect of stream ecology, influencing channel maintenance, clearing of debris dams, promotion of migration and movement of the adults and young of amphidromous native species, cues for reproductive cycles of stream organisms, enhancement of primary or secondary production, control of alien species, provision of habitat heterogeneity, and maintenance of benthic communities (March et al. 2003, Brasher 2003). Because flow in many Hawaiian streams is presently diverted (Timbol and Maciolek 1978, Wilcox 1996), understanding human impacts on flow in stream systems is critical for management and mitigation (HCPSU 1990, March et al. 2003). In light of these advances in our understanding of stream function, the goal of our study was to determine how Hawaiian streams fit into this developing framework of stream ecology.

This 3-yr study was undertaken both to establish a sound baseline for ecosystem-level parameters in a Hawaiian stream and to address specific questions relating to flow and variability in flow. General questions were (1) What are the flow characteristics of a representative Hawaiian stream and how are these altered by a diversion system? (2) What are the effects of the hydropower diversion system in Wainiha River on abiotic and biotic parameters in the stream? (3) How do biological parameters in the stream respond to changes in flow, on a long-term basis, seasonally, and at shorter time scales?

To answer these questions we first characterized conditions in Wainiha River with a detailed study of physical and biotic conditions in the stream itself and in the watershed. We then carried out among-site comparisons of selected biological response parameters at the temporal scale of the entire study (3 yr) and seasonally. Finally we conducted correlation analyses to determine if any of the biotic response parameters we studied at larger temporal scales were influenced by flows that had occurred in the days preceding their measurement.

MATERIALS AND METHODS

Site Descriptions

Wainiha River is located on the north side of the island of Kaua'i (Figure 1). It originates at an elevation of about 1,463 m and flows 23 km to the sea. This river is one of the main drainages of the high-elevation Alaka'i wetland. This wetland, popularly called the "wettest spot on earth" receives more than 490 cm of rain annually (Fontaine 1996). The drainage area for Wainiha River upstream of the U.S. Geological Survey (USGS) gauge site (lat. 22° 08′ 20″ N, long. 159° 33′ 38″ W) is about 58 km^2. Total watershed area is approximately 102 km^2. Mean daily discharge

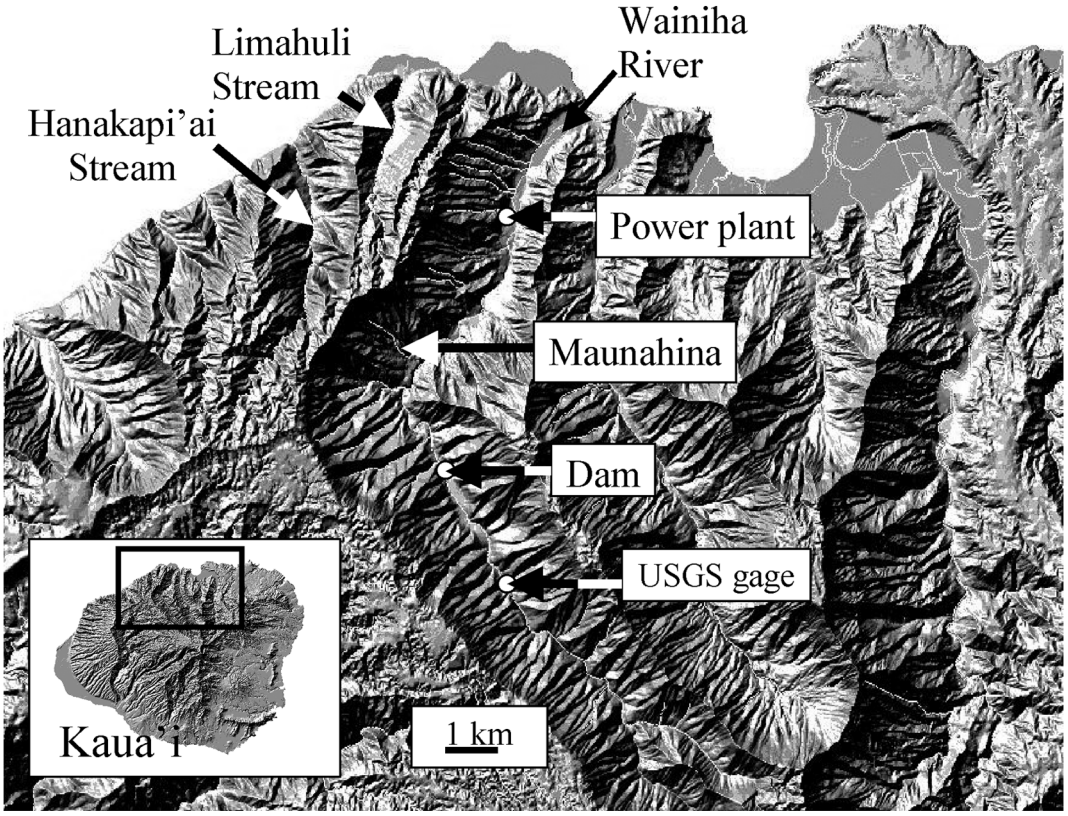

FIGURE 1. Image of the north coast of Kaua'i showing features in Wainiha Valley and neighboring streams. (Image courtesy of M. Kido, Center for Conservation Research and Training.)

(1953–1999) was 3.9 m^3 sec^{-1} (max–min: 793 m^3 sec^{-1}–0.88 m^3 sec^{-1}) (U.S. Geological Survey Water Resources Data Hawai'i). Like many Hawaiian streams constrained within deeply cut valleys (Figure 1), it exhibits a very simple trellis pattern. Inspection of the USGS quadrangle map indicates that Wainiha River reaches the sea as a fourth-order stream. In fact, most of the tributaries shown on the map flow in channels that are often nearly vertical, and many contain surface water only during rain events. In effect this makes Wainiha River functionally a second- or third-order stream. This suggests that stream order may not be a useful metric for short, steep island streams, and if this is true, application of the river continuum concept to Hawaiian ecosystems should be undertaken with caution.

The study was designed to take advantage of an electrical power generation operation that removes surface water from the main channel by a diversion dam at 213 m in elevation, then returns the water to the stream from the powerhouse at 30 m. Four sites on the main channel were chosen to represent reaches with reduced (below the dam and above the power plant), undiverted (above the diversion dam), and restored (below the power plant) flow. Each of the main channel study reaches was 60 m long. In addition some data were obtained from two small tributaries. The six sites are described here:

AD SITE (above diversion dam): This site, at an elevation of 215 m, is located about 8.9 km from the mouth of Wainiha River, approximately 100 m upstream of the diversion dam. Flow at the AD site is unaltered,

and this reach is typical of many Hawaiian streams at similar elevations. The site is situated far enough upstream of the diversion that it is not usually influenced by pooling behind the dam. The streambed is open with no canopy cover over the channel.

BD SITE (below diversion dam): This site, at an elevation of about 207 m, is located approximately 6 m lower than the diversion dam and about 100 m downstream of it. During low flow conditions, all the water is diverted to the power plant so that none flows over the dam. Water sources at this site in these conditions include seepage through and under the dam and groundwater-fed seeps along the banks. At higher discharges water flows over the dam, dramatically changing conditions at the BD site. There is no canopy cover over the channel, although vegetation reaches to the stream margin on one bank but does not shade this reach.

AP SITE (above power plant): This site is at an elevation of about 43 m, approximately 500 m upstream of the power plant and 2.7 km from the stream mouth. Water sources include any flow over the dam into the main channel, as well as water from tributaries and seepages along the stream course below the dam. However, several tributaries are intercepted and diverted to the power plant at higher elevations along the northwest valley wall. The streambed here is wide with no canopy cover. Conditions at this site are representative of many Hawaiian streams that are partially diverted.

BP SITE (below power plant): This site, at an elevation of about 18 m, is approximately 1 km downstream of the power plant and 1.2 km from the stream mouth. Output from the tailrace of the power plant upstream of this site restores volume of flow to that which would exist without the upstream diversion, although water quality may not be typical of such a low elevation site. The study reach is on the northwest side of an alluvial island in the broad valley floor and represents one branch of the Wainiha River, which at this elevation is divided into two main channels. Both margins of the stream are overhung with dense vegetation, but the central part of the channel is open.

TRIBUTARY (TRIB) SITE: In addition to the four sites in the main channel (called main stem here), a fifth site, at 230 m elevation, was located on a small, first-order tributary that enters Wainiha River at about 180 m. The site is above the point where water from this tributary is diverted into the water collection system for the power station. The small channel is completely covered by canopy.

MAUNAHINA STREAM: A named tributary of the Wainiha River is intercepted at an elevation of 219 m by the diversion system (Figure 1). Where the tributary flows into the system there is a grate that collects large litter. We sampled organic litter from this grate during the course of the study. Area of the watershed above the collection grate for this tributary is 0.67 km^2.

Data Sources and Collection

Discharge in Wainiha River is recorded by USGS gauge no. 16108000 located 2.2 km upstream of the diversion dam at an elevation of 293 m. Although there is substantial input into the stream below this gauge, these discharge data reflect the basic flow characteristics of Wainiha River (Figure 2*A*). For our study, we used the annual discharge data reports for this gauge published by USGS (U.S. Geological Survey Water Resources Data Hawai'i) and archived on their Web site (http://waterdata.usgs.gov/hi/nwis/nwisman?site_no=16108000), which provides historical discharge data. We established stage stations at each site on the main stem and calibrated them from direct measurement of flows using a current meter (Swoffer Model 2100) on a top-setting wading rod deployed along a meter tape stretched across the stream. Relationships between measured flows and stage height at the four study sites were determined. At each visit to the main study sites we estimated discharge using the stage gauges once they were calibrated. Correlations between measured flows at the four sites and the USGS gauge data (termed "USGS flows" in this report) were as follows (Pearson's r): AD, 0.67; BD, 0.14; AP, 0.59; BP, 0.39. As expected, correlations decreased

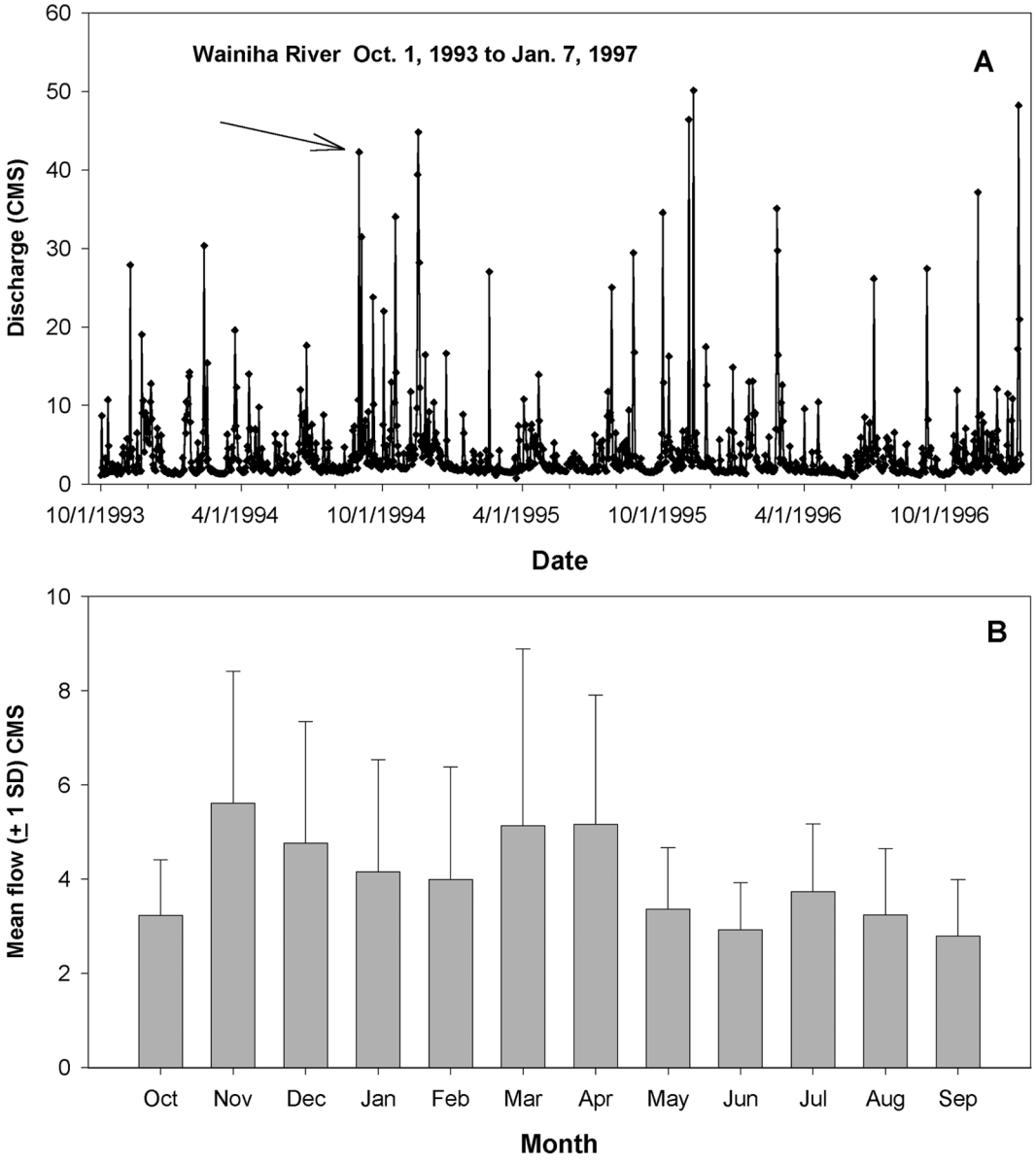

FIGURE 2. Flows in Wainiha River (m^3 sec^{-1}). The data are from USGS gauge station 16108000 (U.S. Geological Survey Water Resources Data Hawai'i). *A*, Daily flows during the study period (1 October 1993–7 January 1997). The arrow indicates the high water event of 2–4 September 1994 that damaged the diversion dam (see text). *B*, Mean monthly flows (±1 standard deviation) in Wainiha River. Data are for 1953 to 2001 (U.S. Geological Survey Water Resources Data Hawai'i).

with increasing distance from the gauging station. The BD site had the lowest correlation because at low USGS gauge flows no water passed over the dam. For the BD site "corrected" flows (i.e., using 0 m^3 sec^{-1} for flows below the dam when USGS flows were below the threshold) were used in analyses. The low correlation at the BP site was proba-

bly due to the fact that at this elevation there is another channel that carries an approximately equal volume of water (our unpubl. data). Unless specifically noted, all analyses and comparisons in this report were made using the USGS gauge daily discharge data. Daily precipitation was recorded at the U.S. Weather Service rain gauge (station HI-41) at the power station (elev. 30 m) (National Oceanic and Atmospheric Administration [NOAA], www.prh.noaa.gov/hnl/hydro/hydronet/hydronet-data.php).

Light was measured at the AD and AP sites. Incident light, as illuminance, was recorded at 1-hr intervals 24 hr a day using data loggers (HOBO, Onset Computer Corporation). These instruments record light in lux (lumens m^{-2}). This is a photometric, not a quantum, measurement, but because only natural sunlight was incident at these sites, and because we used the data only for between-site comparisons, this is not a major concern in this study. Thus, the light values can be taken as an index of incident solar radiation.

We quantified substratum types by dividing the four main-stem study sites into 2 by 2 m quadrats using ropes laid across the stream and 2-m lengths of flagging tape set at 2-m intervals across the channel to demarcate 4-m^2 areas of the streambed. At each site a 40-m reach was selected as a representative area. At the AD and BD sites the width surveyed included parts of the streambed that were sometimes dry but that were frequently submerged. At the two low-elevation sites, streamside vegetation precluded this. Two individuals evaluated each of the 4-m^2 squares assigning percentage cover estimates to each of the bottom types. The same two observers collected the data in 1996 and 1997. The scores given by the two observers for all quadrats were averaged to obtain the substratum size class distribution for each site.

Water temperature was recorded at 1-hr intervals, first with recording thermographs (Ryan), then, starting in January 1995, with submersible digital temperature data loggers (Onset Computer Corporation). On each visit to a site we also measured water temperature and conductivity using a salinity-conductivity-temperature meter (Yellow Springs Instruments model 33). We collected nutrient data on 9 days chosen to represent the entire year as well as a range of flows. Parameters measured were inorganic phosphorus (PO_4^{-2}), nitrate (as $NO_2^- + NO_3^-$), ammonia (as $NH_3 + NH_4^+$), dissolved organic phosphorus, dissolved organic nitrogen, total dissolved organic carbon, total dissolved nitrogen, total dissolved phosphorus, and silicate (SiO_2). We collected water samples using an acid-washed plastic syringe fitted with a GF/C filter. Water was transferred to acid-washed plastic bottles that were first rinsed with some of the filtered sample, and immediately placed on ice in the dark. Samples were kept frozen until they were analyzed. Water analysis was carried out using the methods described in Smith et al. (1981).

We used two measures of benthic standing stock of organic matter at each station: concentration of photosynthetic pigments and ash-free dry mass (AFDM), which includes all benthic particulate organic material. Samples were taken at the four main-stem sites at approximately monthly intervals for a total of 30 samples over the course of the study. Five basalt cobbles (ca. 15–20 cm diameter) were selected from randomly chosen locations in the study reaches using pocket calculator–generated random numbers to choose the spots. The cobbles were brought to the stream bank where the sample was taken from the upper rock surface. Samples were collected using a plastic cylinder (2.6 cm in diameter) fitted with a ring of neoprene rubber glued to the bottom so that it made a tight seal when pressed against the rock surface. About 10 ml of water was added to the tube as it was being pressed to the rock surface and all attached material was loosened using a stiff brush. The slurry of benthic material along with the water was collected with a pipette. This process was repeated three times and the three 10-ml rinses were pooled and placed on ice until they could be processed. A test using multiple serial rinses showed that this method collected 90–92% of the total chlorophyll *a* (chl *a*) in the circular area. The iced samples were returned to the laboratory where they were filtered onto

pre-massed, ashed GF/C glass fiber filters and placed in 12-ml centrifuge tubes and kept frozen until analysis. To obtain pigment measurements, 10 ml of 90% acetone was added to the filters, and the samples were sonicated on ice for two 15-sec bursts using a sonicator (Heat Systems). The samples were then allowed to extract overnight in the dark at −16 °C, centrifuged at 700 g to sediment particles, and analyzed using a diode array spectrophotometer (Hewlett-Packard). Pigments (chl *a*, chl *b*, chl $c_1 + c_2$, and carotenoids) were analyzed using the equations of Jeffery and Humphry (1975). After spectrophotometric analysis, the solvent was returned to the centrifuge tube with the particulates and the filter, and the total sample was poured into ashed, pre-massed aluminum pans. Pans were dried overnight at 60 °C, the dry mass determined, then ashed at 500 °C for 4 hr to obtain the ashed mass. AFDM was the difference between the dry mass and the ashed mass.

Because complex factors can influence standing stock of the benthic photosynthetic assemblage, the use of instantaneous biomass measures (e.g., chl *a* or AFDM) as surrogates for actual productivity rates can be misleading. To estimate net primary productivity more directly we measured the increase of photosynthetic biomass (as fluorescence) over short time intervals. Unglazed 5 by 5 cm ceramic tiles were placed in the stream attached to concrete blocks or large boulders using self-closing tape (Velcro) glued to the boulders and tiles. At approximately weekly intervals, sets of three tiles were retrieved and the accumulated chlorophyll was estimated using fluorescence of a known volume (10 ml) of 100% methanol extract (data for these experiments are fluorescence units, not chl *a*). Because these tiles were uncaged, there was no protection from grazing, so the pigment levels represent net accumulation, not gross production. Our goal was to carry out replicated time trials in both summer and winter during the course of this study. However, many of the tile runs were destroyed by high flows, so only six were complete enough to analyze.

Plastic trays (0.16 m^2) were placed at the four main-stem sites and the tributary site. In 1994 there were five trays at each site. For the remainder of the study the number of trays at the four main-stem sites was increased to 15. The TRIB site had five trays during all years. The trays were located in vegetation types that were characteristic of the riparian vegetation at each site. Trays were checked about every 2 weeks and any plant material that was in a tray was collected and taken to the laboratory, where it was sorted into major species groups. The plant material was then dried at 60 °C and massed to obtain dry mass.

We collected litter from a flume grate on Maunahina Stream, a small tributary of Wainiha River (Figure 1). The tributary is intercepted at this site and its water diverted to the flume for the water collection system. The intake for the flume is protected by a grate to screen out large detritus. Openings in the grate hold back most material greater than about 3 cm. Periodically we collected all material accumulated on this grate. Wet mass of the entire collection was determined, a subsample taken, and after determining its wet mass, it was dried at 60 °C and massed. Total mass of the entire sample was determined by back calculation.

We conducted five litter bag studies in the TRIB site using closed, mesh (7 mm stretched) bags containing known amounts of dried (60 °C for 24 hr) guava leaves (*Psidium guajava*) to estimate leaf litter breakdown. Decomposition rates were estimated using a negative exponential decay model (McArthur et al. 1994) where mass remaining $= C^* e^{-kt}$. C is a constant (1 if percentages are used), t is the time the leaf bags are immersed, and k is the decomposition rate.

Until May 1994, benthic invertebrates were sampled using a Surber sampler (area 0.093 m^2) that was only effective in shallow (<30 cm) water, so sample locations were limited to this depth. After that date we used a Hess sampler (area 0.085 m^2), which allowed us to effectively sample in deeper water. Samples taken after May 1994 were located at five randomly selected spots in each of the four study reaches. Material was removed from the substratum by first overturn-

ing all loose rocks within the sampler area, then scrubbing all hard surfaces with a stiff brush. Samples were collected in the net (100-μm mesh size) attached to the sampler and immediately fixed in formalin. Subsequently, samples were sorted to the lowest possible taxon and enumerated. Dry mass (60 °C) was obtained for each taxon in the sorted samples. For very large samples that were subsampled before enumeration, total dry mass was obtained by multiplying the dry mass of the enumerated fraction by the dilution factor. Abundance and biomass data for the benthic samples were normalized to 1 m^2. Because of the possibility that simply accounting for total numbers and biomass of benthic invertebrates might not detect changes in community structure, diversity of the benthic samples was determined using the Shannon-Wiener function H' (e.g., Krebs 1985) measure of diversity. Diversity was calculated separately for abundance and biomass data.

On each sampling date, three 20 cm diameter (150-μm mesh) plankton nets were used to collect drifting invertebrates at each site. Total stream discharge at the site was measured while the nets were deployed so that the catch could be normalized to total volume of water passing that point (number or dry mass per unit time for the entire river). Nets were deployed for 20 min and velocity at the mouth of the nets measured with a current meter (Swoffer). Samples were treated in the same manner as the benthic invertebrate samples. As with the benthic invertebrate samples, data are reported both in terms of abundance and biomass, as well as the diversity of these parameters. We used the site-specific discharge taken while the drift samples were being collected for these calculations, but we had to use the USGS daily records for the cross-correlation analyses because we did not manually take discharge or record stage at each site every day. Drift samples were collected during daylight hours, so they may not reflect total drift (Barnes and Shiozawa 1985).

The movement of particulate material downstream is an intrinsic feature of lotic systems. The movement and processing of particulate material is a fundamental component of the river continuum concept (Cummins 1974, Elwood et al. 1983, Fisher et al. 1998). One prediction of this model is that as organic material is transported downstream, the processing (chemical and mechanical) by the stream biota gradually reduces the size of organic particles. We tested this hypothesis by comparing the ratio of coarse particulate organic matter (CPOM) to fine particulate organic matter (FPOM) at the four sites along the main stem, with the prediction from the model being that the FPOM: CPOM ratio should increase downstream. We sampled drift at each site using drift nets with a mouth diameter of 20 cm and a mesh size of 150 μm. Water velocity at the mouth of the net was taken as for the drift samples. The material collected was concentrated and taken to the laboratory, where it was put through a sieve with a mesh size of 1,000 μm. Material retained on the sieve was greater than 1,000 μm and termed CPOM; the material that passed through the sieve was collected and represented FPOM. Both fractions were dried at 60 °C, massed, then ashed to obtain AFDM as a measure of organic content of the transported load.

Analyses

We examined the data in three ways. First, data are presented as values (usually medians in graphs and means $\pm$ 1 standard deviation in tables) over the course of the 3-yr study. Usually no further analyses of the data across the entire sampling study were undertaken unless there appeared to be a trend over the 3-yr data set. Second, we analyzed among-site differences. Unless otherwise noted, among-site differences were analyzed using one-way repeated measures analyses of variance (ANOVAs). In cases where variances were very different among sites, data were transformed, but all results are presented in terms of untransformed values. When variances could not be stabilized, nonparametric tests were used. Post hoc (Duncan's) comparisons were used to test differences among means for the parameters at the four sites, with α set to 0.05 unless

otherwise noted. For some parameters summer versus winter season data were compared across sites using two-way repeated measures ANOVA. We defined summer or warm season as May through October and winter or cool season from November through April. Because there were only 30 sampling days during the entire study for most parameters, the data were not suitable for any more sophisticated time series analyses of seasonality.

A direct result of stream diversion is a change in discharge downstream of the diversion. Because of this, a central question in our study was whether flow events might affect biological parameters. To investigate this possibility we used correlation analyses to test whether biological parameters responded to flow history at a site using a time series analysis based on correlations of the parameter of interest with the discharge on the day the biological data were taken (day 0), 1 day previously (day 1), and so on to the final correlation between the biological parameter and the flow 30 days earlier (Lai 1979).

Proper interpretation of these analyses requires an understanding of how the correlation values were generated, so we present the procedure in some detail here. For each biological parameter we measured (e.g., median benthic chl *a*) we had 30 sample days during the 3-yr study. Sampling was at approximately 30-day intervals, though some intervals were substantially longer due to inclement weather, and a few were shorter. To obtain the day-0 correlation coefficient (Pearson's *r*), a pairwise correlation was calculated between each of the 30 parameter values obtained on the 30 sampling days and the 30 USGS flows recorded on the same day. Note that the among-site correlations were not independent of each other because all used the same USGS discharge data set. For the BD site, discharge was set to 0 (designated as "corrected" in graphs) for days when there was no flow over the dam as determined from the flow duration curve (see later in this section). The day-1 lagged correlation was calculated in the same manner using the same 30 parameter values, but now correlated with the 30 USGS flows recorded for the day before the samples were collected. Thus, because all the cross-correlation analyses used the same parameter value for each site for each of the 30 lag calculations, within-site data were also not independent. This procedure was repeated up to a lag of 30 days. Sample size for each of the correlation calculations was generally 30 because there were 30 samples of each parameter taken during the entire study.

How are these analyses to be interpreted? A high positive correlation between, for example, chl *a* and flow on day "*N*" means that either high benthic chl *a* is associated with a high flow at that lag, or low chl *a* is associated with low flow at that lag. Because each correlation coefficient is based on 30 sample days, both situations could be contributing to the high value. Similarly a strongly negative correlation would indicate that chl *a* was reduced when high flows preceded the measurement by *N* days or was high when low flows preceded the measurement by *N* days. It is important to remember that each of these correlation values was based on the 30 sampling occasions spread over the 3-yr study, so in one month there might have been a high flow *N* days before the chl *a* sample was collected, but the next month a low flow might have preceded the sampling by *N* days.

Significance of these peaks was determined following Lai (1979). Olden and Neff (2001) discussed several problems involved in time series analyses such as the one we use here. Given their cautions, the results of the cross-correlation studies reported here should be taken as indications of trends and not as explicit statistical tests.

RESULTS

Site Characteristics

Daily discharge was variable, with high flows occurring in any month (Figure 2*A*). During this study there were 12 recorded flows greater than 30 m^3 sec^{-1}. Mean monthly flow during the study suggested somewhat higher flows from November through April (Figure 2*B*). Flow frequency data for the same period (Figure 3*A*) illustrate several points. High

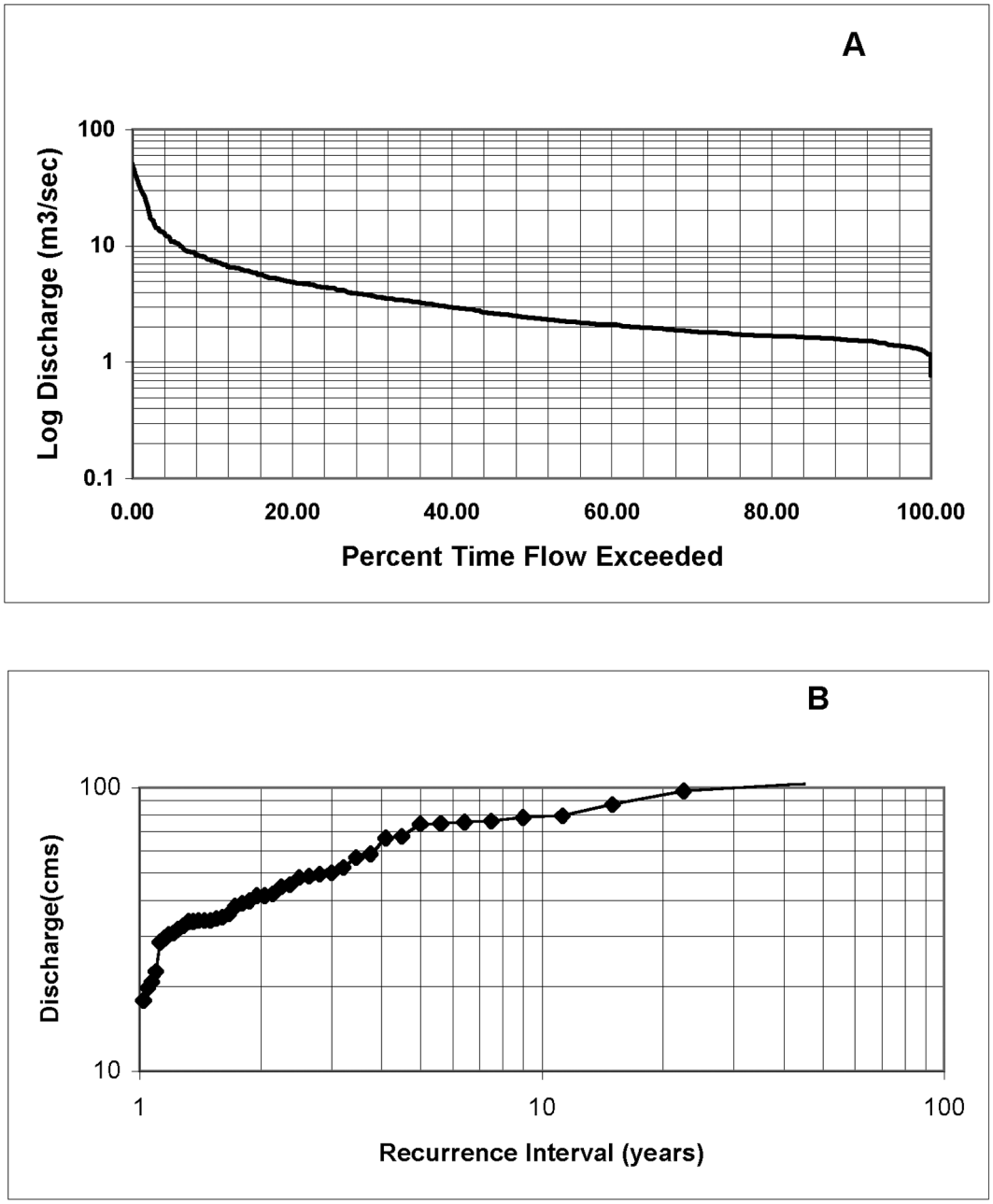

FIGURE 3. *A*, Flow frequency for the Wainiha River for the study period: 1 October 1993–7 January 1997 (U.S. Geological Survey Water Resources Data Hawai'i). *B*, Recurrence intervals for flows of different magnitudes for Wainiha River. Data are from water years 1953–2001 measured at the USGS gauging station.

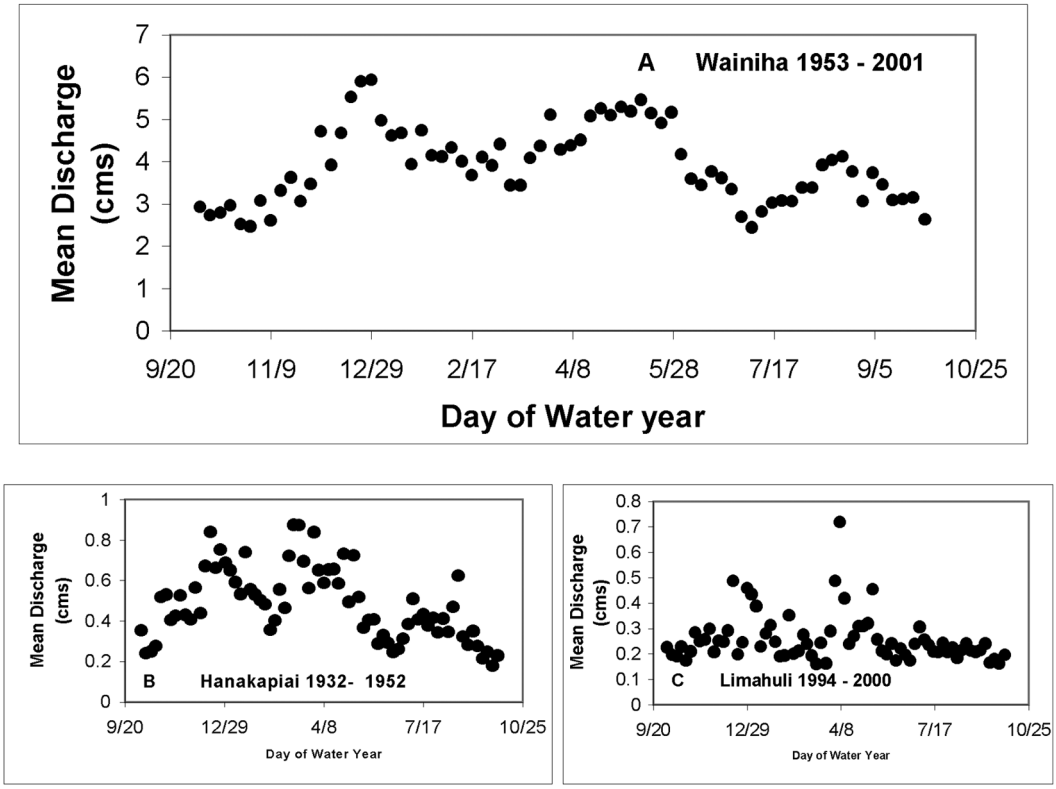

FIGURE 4. Mean discharge for three Kaua'i streams based on 5-day "pentads" (see text for method) of discharge data (U.S. Geological Survey Water Resources Data Hawai'i). Figure 1 shows the location of these streams. *A*, Wainiha River for water years 1953–2001. *B*, Hanakāpī'ai Stream for water years 1932–1952. *C*, Limahuli Stream for water years 1994–2000.

flows (>10 m^3 sec^{-1}) occurred less than 4% of the time. Flow was less than 5 m^3 sec^{-1} on more than 80% of the days during the study period. Analysis of recurrence intervals for flows of various magnitudes (Figure 3*B*) showed that floods of 80 m^3 sec^{-1} may occur at about 10-yr intervals. Oki (2004) suggested that over the 48 yr of record there has been a decrease in flow in Wainiha River.

An unexpected finding was the trimodal discharge pattern (Figure 4) for Wainiha River when data for the 48 yr of record were averaged over 5-day "pentads" (a mean for each of the 73 5-day intervals [i.e., 1–5 October, 6–10 October, etc., across all 48 yr] [see Richards 1979]). Spectral analysis of 48 yr of discharge data indicated that the time series exhibits two main frequencies: one at 1 yr and one at approximately 4 months. Both patterns are reflected in Figure 4. Similar trimodal patterns (Figure 4) are apparent when time series analyses were carried out for two neighboring streams that also receive water from this source (Limahuli and Hanakāpī'ai), suggesting a similar mechanism governing stream flow in this region of Kaua'i.

Our direct observations showed that, before September 1994, no water flowed over the dam at flows less than 2.7 m^3 sec^{-1}, as measured at the USGS gauge. Flows less than that occurred about 55% of the time (Figure 3*A*), so that there was no flow over the dam on more than half the days during that period. From 2 to 4 September 1994 there was a high water event (see Figure 2*A*), which damaged the diversion dam. A sheath

of reinforced concrete was stripped from about 25% of the width of the dam, lowering the level where the damage occurred by about 5 cm. This damage resulted in water flowing over the dam at a lower discharge than previously: about 2.36 m^3 sec^{-1} at the USGS gauge. Consequently, since September 1994 the dam has diverted all water about 45% of the time. Thus, a lowering of the dam by only 5 cm resulted in water passing over the dam about 10% more frequently, or 36 more days per year.

To quantify variability in flow we calculated the ratios of discharge extremes using the metrics in Maciolek and Ford (1987). These ratios are the quotient of maximum daily flow/minimum daily flow (1) for the year (i.e., the year's highest flow divided by the lowest flow recorded that year), (2) during a month (i.e., the highest and lowest flow for each month averaged over the year), and (3) on consecutive days (i.e., the highest ratio between flow in two consecutive days each month, again averaged for the year). Over 48 yr of record for Wainiha River the yearly maximum:minimum ratio was 39.25, the monthly average ratio was 12.05, and the average daily ratio for the entire period was 5.60. When compared with the data in Maciolek and Ford (1987) for Kahana Stream on windward O'ahu, the annual ratio and monthly ratios for Wainiha were somewhat higher (39 versus 29 and 12 versus 11.5) and the ratio for consecutive days was higher in Kahana (9.3 versus 5.6). The daily ratio for Kahana was the highest of all the streams in Oceania that Maciolek and Ford analyzed. These values indicate large and frequent discharge fluctuations. Channel flushing and disturbance of the streambed occur often in streams such as these.

To enlarge the scope of among-stream comparisons, we analyzed the flow data for Wainiha River using the habitat template model of Poff and Ward (1989, 1990). Variables for Wainiha grouped the river in their "perennial flashy" category (data not shown). Discharge patterns in Wainiha River are strikingly similar to their type 3D, exemplified by the "perennial flashy" Satilla River in Georgia (Poff and Ward 1990).

Precipitation during the 3-yr study (Figure 5*A*) was variable both across the water year and among years (shown by the error bars). The 5-day "pentad" data for discharge (Figure 4) and precipitation (Figure 5*B*) from October 1994 to November 2000 show similar trimodal patterns and are positively correlated (r^2, 0.59). This fairly weak correlation is not unexpected because the rain gauge is at a low elevation and so may be unrepresentative of precipitation in the upper watershed.

Total monthly mean daily irradiance (all hourly values for each day first summed, then averaged for each month) was measured from April 1996 to February 1997 (Figure 6*A*). Although data for some months are missing, the winter (November–April) values seem lower relative to the summer (May–October) values at the AP site, and there appears to be less difference at the AD site. When monthly mean total irradiance values for both sites were compared, using only months when data were available from both sites, the AP site did show significantly greater variability in total daily irradiance ($F = 2.87$; df = 139, 177; $P = 5.8\ E^{-11}$). For the same months, using the single highest light measurement for each day in a month, averaged for that month (Figure 6*B*), the AP site also had significantly greater variability in maximum irradiance ($F = 1.60$; df = 141, 178; $P = 0.0032$).

Boulders were the primary substratum type at all but the BP site (data not shown). Substrata at both lower-elevation sites are characterized by relatively more cobble and less boulder than the higher-elevation sites. Substratum determinations were made in 1996 and 1997. There were minor changes between these two sampling dates indicating that, although the overall differences among sites remain, there is some temporal variability in the substratum.

Water Quality Parameters

The diurnal range in water temperature can be greater than 5.5 °C (Figure 7). Flow on the days shown in Figure 7 was quite low: near the 98% exceedence level (USGS discharge 1.2–1.3 m^3 sec^{-1}). The AP site had the highest temperatures and greatest diurnal

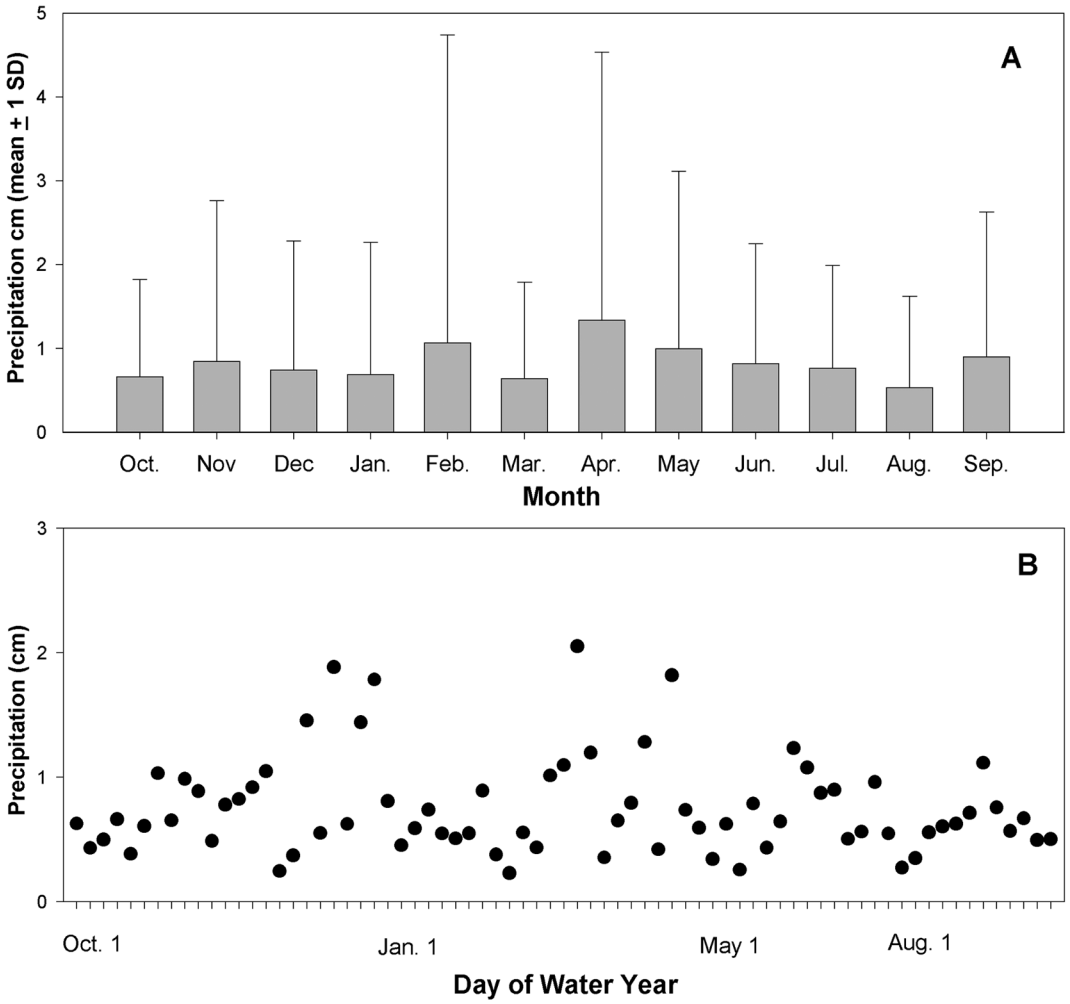

FIGURE 5. Precipitation recorded at NOAA rain gauge HI-41 at the power plant in lower Wainiha Valley (NOAA, www.prh.noaa.gov/hnl/hydro/hydronet/hydronet-data.php). *A*, Mean (±1 standard deviation) precipitation for the 3-yr study period 1 October 1993–7 January 1997. *B*, Precipitation recorded at NOAA gauge HI-41 based on 5-day "pentads" (see text for method).

range of any of the four main-stem sites. At the higher elevation, temperatures on these 3 days at the AD site were consistently higher than at the BD site, which at this low flow was entirely fed by springs and seeps.

There was marked seasonal variation in water temperature at all the study sites (Figure 8). Temperatures were high from May to October and low from November to April. Because the seasonal variations in temperature were much clearer than in precipitation or discharge we use summer or "warm season" (May through October) and winter or "cool season" (November through April) as our two seasonal periods.

Pairwise comparison of noon temperatures among the four main-stem sites for the entire study period showed that variability was significantly higher at the AP site (F tests: all $P < 0.0001$). When all temperature data,

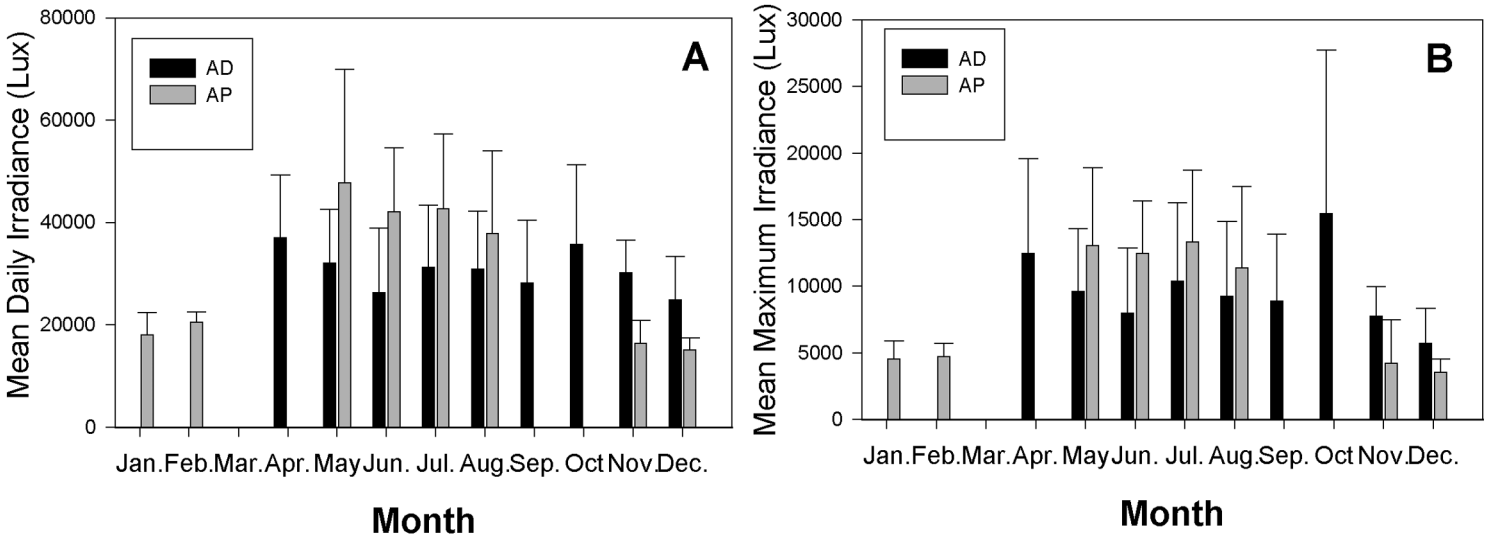

FIGURE 6. Irradiance at the AD (above dam) and AP (above power plant) stations during the 3-yr study. *A*, Daily irradiance (sum of hourly values for each day, averaged over the month) (±1 standard deviation). *B*, Maximum irradiance for each day averaged over the month (±1 standard deviation).

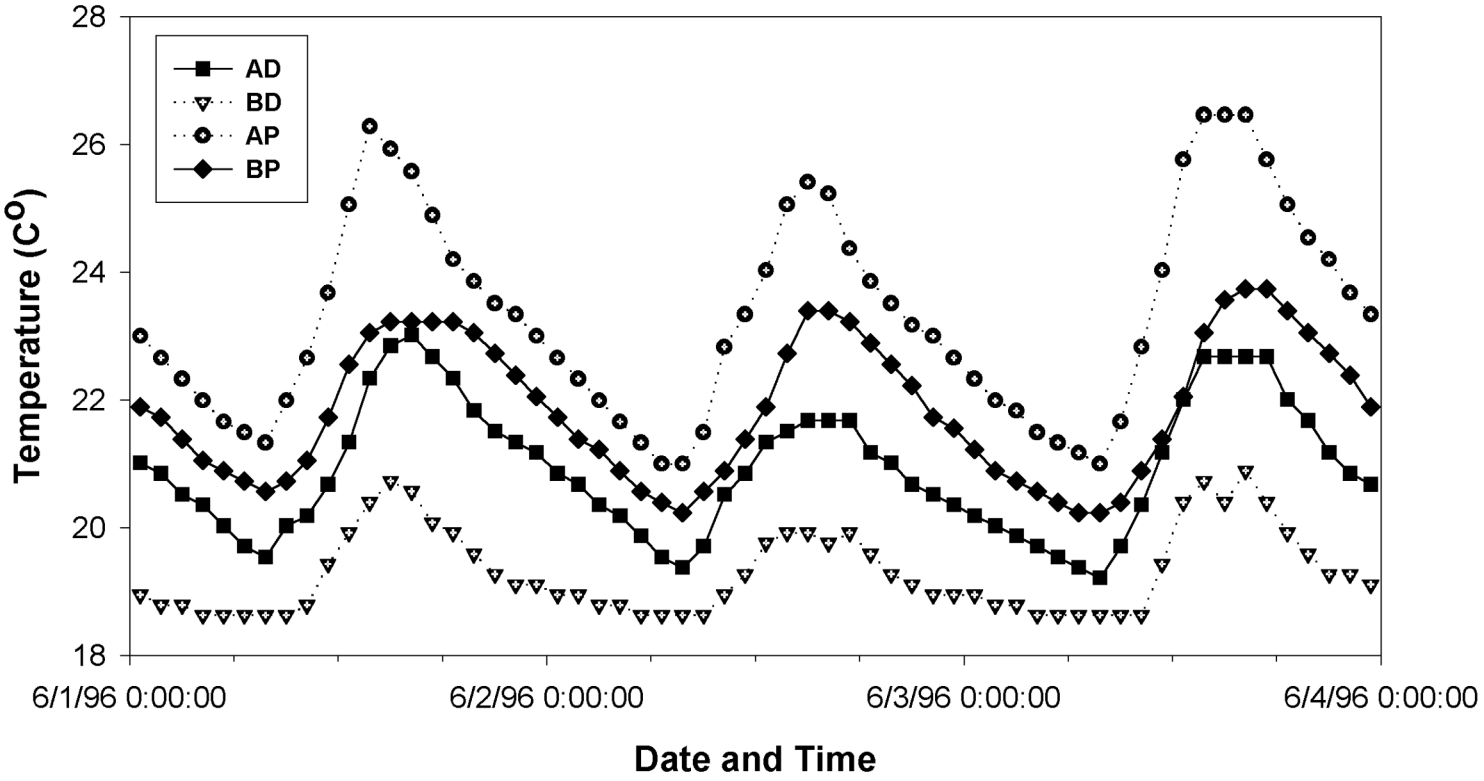

FIGURE 7. Water temperature at the four main-stem study sites from midnight 1 June 1996 to midnight 4 June 1996. Solid symbols represent sites with full flow (AD and BP); open symbols represent sites with reduced flows (BD and AP).

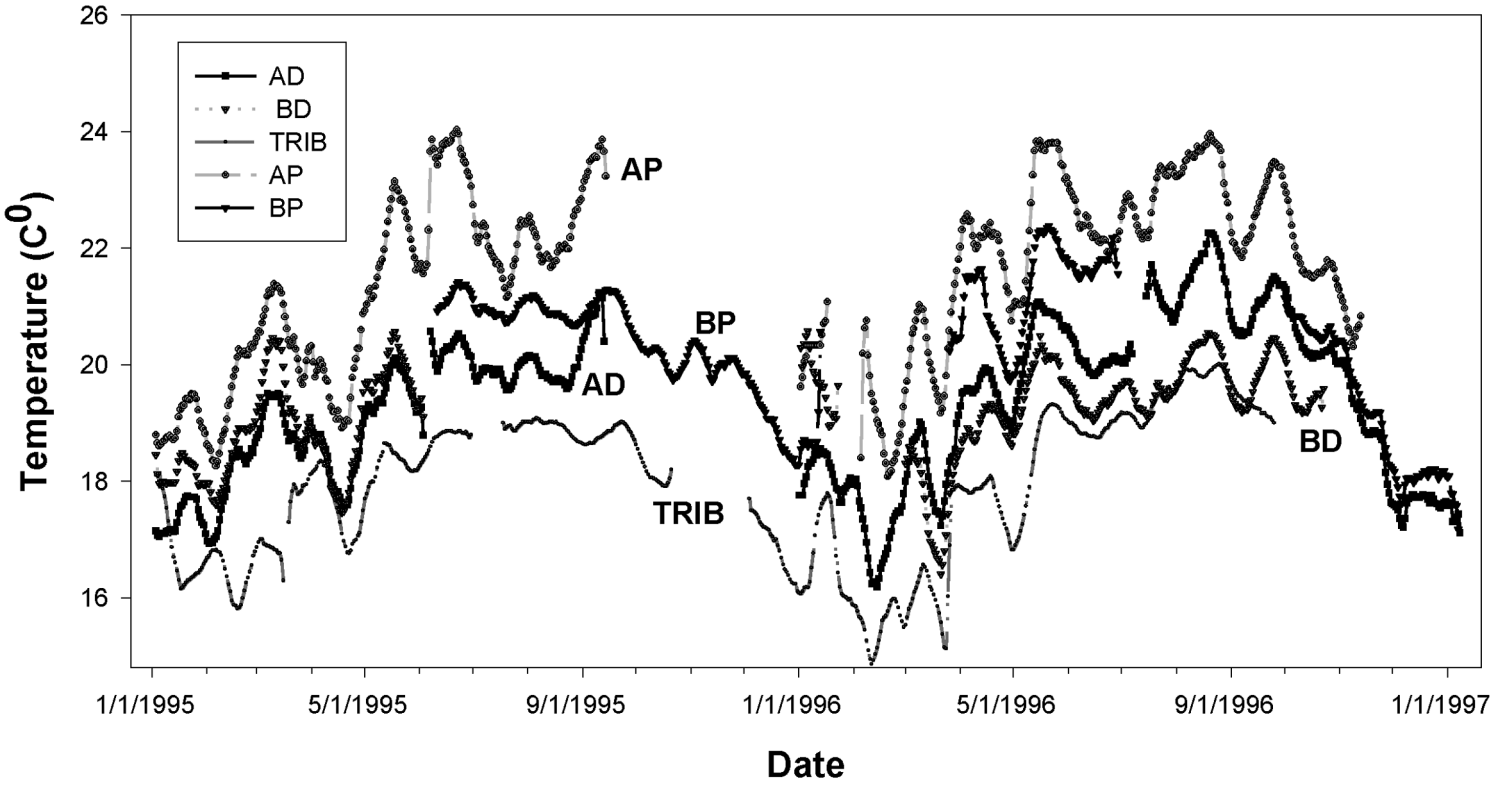

FIGURE 8. Water temperature at the four main-stem sites and the tributary site over the 3-yr study period. Data are presented as 12-day running mean temperatures.

TABLE 1

Mean Nutrient Concentrations in Wainiha River (Data Divided into Dates When USGS Flows Were Less Than 4.0 cm [$n = 6$] and Days When USGS Flows Were Greater Than 4.0 cm [$n = 3$])

	Cond.[a]	PO_4	NO_3	NH_4	DOP	DON	TOC	TDP	TDN	Si
$<4.0\ m^3\ sec^{-1}$										
AD[b]	53.16	0.25	3.00	0.21	0.16	6.51	1.12	0.40	9.72	263.52
BD	60.84	0.28	5.01	0.20	0.13	5.07	1.01	0.41	10.30	280.72
TRIB	60.96	0.31	3.98	0.18	0.11	3.78	0.62	0.42	7.94	343.49
AP	82.81	0.22	1.41	0.25	0.15	5.12	0.92	0.37	6.77	301.64
BP	66.64	0.25	1.87	0.27	0.12	5.13	1.00	0.37	7.26	294.59
$>4.0\ m^3\ sec^{-1}$										
AD	36.83	0.19	3.54	0.33	0.18	9.88	3.27	0.37	13.75	185.71
BD	34.44	0.19	4.37	0.33	0.19	9.32	3.18	0.38	14.01	169.65
TRIB	52.14	0.30	6.60	0.27	0.22	9.39	2.94	0.51	16.26	227.17
AP	60.83	0.23	4.18	0.32	0.21	10.33	3.33	0.44	14.83	188.31
BP	52.14	0.23	4.52	0.39	0.24	10.46	3.35	0.46	15.37	223.13

[a] Cond., conductivity in $\mu S\ cm^{-1}$; PO_4, orthophosphate, μM; NO_3, nitrate + nitrite, μM; NH_4, ammonium + ammonia, μM; DOP, dissolved organic phosphorus, μM; DON, dissolved organic nitrogen, μM; TOC, total dissolved organic carbon, μM; TDP, total dissolved phosphorus, μM; TDN, total dissolved nitrogen, μM; Si, silicate, μM.

[b] AD, above-dam site; BD, below-dam site; TRIB, tributary site; AP, above–power plant site; BP, below–power plant site.

including those from the tributary site, are compared, among-site differences were significant (ANOVA using natural log-transformed data $F = 414.59$, $df = 4$, $P < 0.0001$). Post hoc tests indicate that the lower-elevation sites had the highest temperatures (AP > BP > AD = BD > TRIB). The approximately 0.5–1 °C lower temperature at the BP site relative to the AP site 1.5 km upstream was probably due to the fact that, at the power station, a large volume of relatively cool water from the diversion dam is replaced into the main stream.

Conductivity exhibited significant differences among stations, with a trend of increasing conductivity from high elevations to low elevations at both high and low flows (Table 1). However, at the lower elevation conductivity at the AP site was 1.24 times higher than at the BP site 1.5 km downstream. When data from the entire study are combined, conductivity at the BP site, where the water is a mixture of water received from the AP site upstream and the water diverted by the dam to the flume system, was almost exactly equal to the mean of the conductivities at the AD and AP sites. The two sites with reduced flow (BD and AP) had similarly high variability in conductivity as estimated by F tests of sample variance ($F = 1.16$; $df = 74, 74$; $P = 0.52$). At the lower elevation, variance in conductivity at the sites with low flow was significantly greater than at the sites with full flow (AP versus BP) ($F = 2.42$; $df = 72, 74$; $P = 0.002$). Variability in conductivity at the TRIB site was significantly lower than at both sites with reduced flow (BD and AP both $P < 0.02$).

Conductivity at all four main-stem sites was lower during high flows than during low flows (Table 1) as measured at the USGS gauging site. Linear regressions of specific conductance at the four main-stem sites versus USGS discharge are all significant (slopes for sites with normal flow [AD and BP] < -2; slopes for reduced-flow sites [BD and AP] < -5.0, all $P < 0.0008$). It is not surprising that conductivity at the tributary site showed no relationship with flow gauged in the main channel ($r^2 = 0.05$, $P = 0.12$). The data set is probably biased because as discharge increased there were fewer measurements, both because there were fewer days with very high flows and because of the danger inherent in accessing the sites during storms. At the BD site conductivity was, on average, 30% higher when there was no flow over the dam than when water flowed over it. Even at the AP site, which showed the highest conductivity in our study, mean

values were generally less than those in neighboring smaller streams (Paul et al. 2004).

We predicted that the inorganic nutrients would show the same relationship with discharge as conductivity because of dilution effects, that dissolved organic material would increase with flow as more organic material was washed into the stream during rainfall, and that at very high flows organics would be released from cell damage due to scouring. There was a negative relationship at all sites between the concentration of silicate and discharge as recorded at the USGS gauge, but slopes were significant only at the sites with reduced flow (BD [$r^2 = 0.47$, slope = -41.03 ± 14.24, $P = 0.024$] and AP [$r^2 = 0.57$, slope = -39.73 ± 11.62, $P = 0.011$]). In a study on much smaller streams on O'ahu, Larned and Santos (2000) also showed a decrease in conductivity during high water events, though Laws and Ferentinos (2003) found the opposite trend in some very eutrophic O'ahu streams. Hoover (2002) reported that nutrient concentrations generally declined with increasing flow, but that, except for Waikele Stream, an urban O'ahu stream, the relationships were weak. He did report that in Waimea (Kaua'i) and Kalihi (O'ahu) streams, nitrate concentrations seemed to increase with discharge.

As predicted, the concentration of total organic carbon at all the stations showed a positive relationship with USGS discharge data. This relationship was significant (all $P < 0.005$) at the four main-stem sites. There was also a significant positive relationship between total dissolved organic carbon and discharge at the tributary site ($P = 0.02$), but because this tributary is not influenced by the flow in the main stem where the gauge is located, this weaker relationship is not surprising. If site-specific discharge values are used instead of the USGS flows the relationships for the main-stem sites are not as strong, suggesting system-wide rather than reach-specific processes.

Differences in water chemistry among all five sites were evaluated using one-way ANOVA. Phosphate, nitrate, and total dissolved phosphorus showed significant among-site differences (PO_4: $F = 2.86$, df = 4, $P = 0.044$; NO_3: $F = 3.39$, df = 4, $P = 0.024$; TDP: $F = 3.22$, df = 4, $P = 0.029$). A posteriori tests suggested that the AP site had the lowest concentrations and the tributary site had the highest levels of phosphate and total dissolved phosphorus. Nitrate was also highest at the tributary and lowest at the two low-elevation sites. There were no among-site differences for ammonia concentration, total dissolved nitrogen, silicate, or total organic carbon, dissolved organic nitrogen, or dissolved organic phosphorus (all $P > 0.1$). Two-way ANOVAs with flow (full [AD and BP] or reduced [BD and AP]) and elevation (high [AD and BD] or low [AP and BP]) indicated no among-group differences (all $P > 0.09$). Generally nitrate, total dissolved nitrogen, phosphate, and total dissolved phosphorus concentrations in Wainiha River were similar to those reported by Paul et al. (2004) in the neighboring Limahuli and Hanakāpī'ai Streams, though their ammonia concentrations were all, unaccountably, below our detection levels. Wainiha nutrient levels were generally much lower than in O'ahu streams (Hoover 2002, Laws and Ferentinos 2003) and central O'ahu groundwater (Hunt 2004), and similar, including ammonia concentrations, to those in small, noneutrophic O'ahu streams (Larned and Santos 2000) as well as in streams on Maui, Moloka'i, and Hawai'i (Hoover 2002). Wainiha nutrient concentrations are similar or lower than those reported for other small, tropical streams as well (McDowell et al. 1995, Chestnut and McDowell 2000).

Benthic Plant Material and Biomass

There was an increase in benthic chl *a* during the duration of the study at the two sites with full flow (AD and BP) (Figure 9*A*). The trend, based on linear regression of chl *a* against sampling date, was positive and significant at both these sites (AD: $r^2 = 0.53$, slope = 0.0037 ± 0.001, $P = 0.0037$; BP: $r^2 = 0.13$, slope = 0.007 ± 0.002, $P < 0.0001$). This slight but significant increase in chl *a* began in the fall of 1994. Neither of the two sites with reduced flows (BD and AP) showed any trend over the study period (BD:

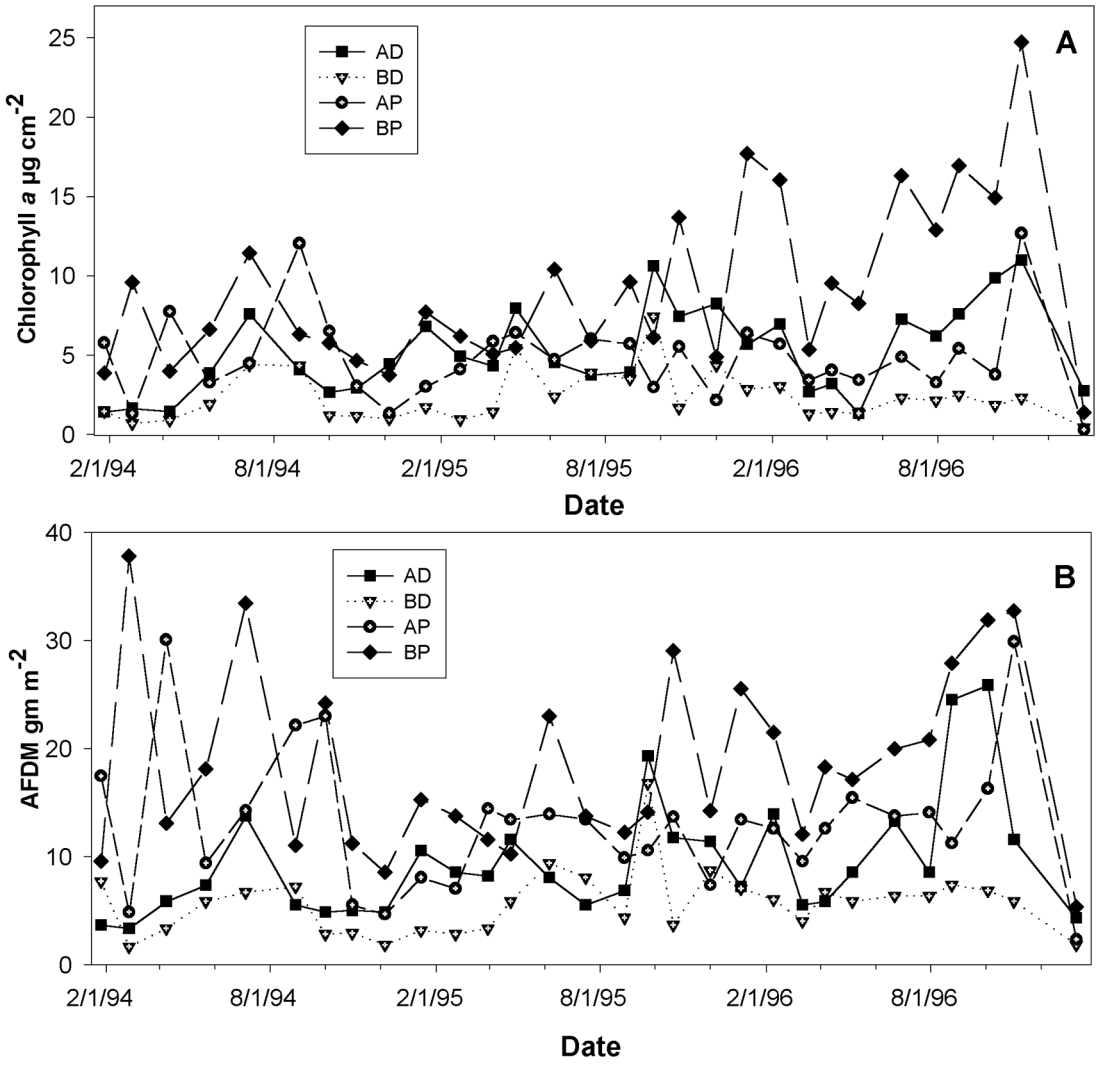

FIGURE 9. Median values for benthic parameters from cobbles at the four main-stem study sites over the course of the study. Solid symbols represent sites with full flow (AD and BP); open symbols represent sites with reduced flows (BD and AP). *A*, Chlorophyll *a*. *B*, Ash-free dry mass.

$P = 0.43$; AP: $P = 0.34$). The timing of the increase at the AD and BP sites is roughly coincident with the reduction in height of the dam, but it is not clear how that event would impact the two sites with undiverted flow.

The accessory pigments (chl *b*, chl *c*, and carotenoids [data not shown]) showed trends similar to those seen for chl *a*, with increasing levels during the course of the study at the full-flow AD and BP sites but not at the two sites with reduced flow. The positive slopes for the three accessory pigments at the AD and the BP sites are all significant ($P < 0.05$) except for chl *b* at the AD site ($P = 0.088$). None of the accessory pigments showed significant trends at the two reduced-flow sites (all $P > 0.17$).

Ash-free dry mass increased over the

TABLE 2

Benthic Plant Pigments (Mean ± 1 SD) and Ash-Free Dry Mass (AFDM) at the Four Study Sites Totaled across the Entire Study Period

	chl *a* ($\mu g\ cm^{-2}$) (mean)	chl *a* ($\mu g\ cm^{-2}$) (median)	chl *b* ($\mu g\ cm^{-2}$)	chl *c* ($\mu g\ cm^{-2}$)	Carotenoids ($\mu g\ cm^{-2}$)	AFDM ($g\ m^{-2}$)
AD	6.21 ± 4.76	5.26 ± 2.76^{B}	1.07 ± 1.04	0.753 ± 0.353	0.806 ± 0.350	10.25 ± 7.48^{C}
BD	3.07 ± 3.57	2.39 ± 1.59^{C}	0.554 ± 0.701	0.483 ± 0.233	0.543 ± 0.285	6.86 ± 7.00^{BD}
AP	5.04 ± 3.55	4.86 ± 2.68^{B}	0.560 ± 0.337	0.774 ± 0.429	0.861 ± 0.331	14.10 ± 15.93^{B}
BP	9.70 ± 6.30	9.18 ± 5.36^{A}	1.28 ± 1.29	1.40 ± 0.808	1.31 ± 0.530	21.04 ± 15.47^{A}

Note: The two values for chlorophyll *a* are based on the mean of the five samples taken on each sampling date (mean) and the median of the same five samples (median). Values followed by the same superscript letter are not significantly different ($\alpha = 0.05$).

course of the study (Figure 9*B*). When natural log of AFDM is regressed on sampling day, the high-elevation sites showed significant increases over the duration of the study (AD: $r^2 = 0.062$, slope $= 0.0006 \pm 0.0002$, $P = 0.0012$; BD: $r^2 = 0.024$, slope $= 0.0004 \pm 0.0002$, $P = 0.035$), whereas slopes were positive but not significant at the two lower-elevation sites (both $P > 0.1$). Thus, the temporal patterns for AFDM are similar to those for chl *a*.

Comparisons of the four main-stem sites across all sampling dates (Table 2) show differences among sites for all the benthic parameters measured. A repeated measures ANOVA for chl *a* and AFDM (both natural log-transformed) showed that the among-site differences were significant (chl *a:* $F = 25.3$, df $= 3$, $P < 0.0001$; AFDM: $F = 26.8$, df $= 3$, $P < 0.0001$). The overall date-by-site interaction was not significant for chl *a* or AFDM ($P = 0.3$ and 0.1, respectively).

A posteriori among-site comparisons for benthic chl *a* show that the BP site had the highest levels of plant pigment and the BD site had the lowest levels. The AD and AP sites were intermediate and did not differ from each other (Table 2). Benthic AFDM differed among all four sites. AFDM was also highest at the BP site and lowest at the BD site. The AP site ranked below the BP site and above the AD site for this parameter. Benthic chl *a* values from nearby Hanakāpīʻai and Limahuli Streams are similar or somewhat higher than the levels in Wainiha (Paul et al. 2004), and the benthic AFDM in Wainiha is similar to that reported from other small tropical streams (Resh and De Szalay 1995).

Because of the overall differences among the sites it is useful to adjust the total values of the pigments to determine if there are any changes in the community composition, aside from the overall differences in total pigment. The ratio of chl *a* to AFDM gives a rough indication of how much of the total organic matter in the benthic aufwuchs (as estimated by AFDM) is contributing to primary productivity (as estimated by chl *a*). A low chl *a*:AFDM ratio indicates a dominantly heterotrophic assemblage, whereas high values of this ratio indicate that photosynthesis may be important. Repeated measures ANOVA on natural log-transformed measurements indicated that there were significant differences among the four sites in terms of the amount of chl *a* per unit of organic benthic biomass ($F = 26.75$, df $= 3$, $P < 0.0001$). A posteriori tests indicated that the AD site had the highest proportion of photosynthetic pigment in the organic aufwuchs (Table 3).

The most appropriate way to test for seasonality is time series analysis. However a basic assumption for most time series analyses is that the data are collected at equally spaced time intervals. Because logistics prevented us from such a precise sampling schedule, problems could arise in the analysis. Also, with only 30 benthic samples spread over 36 months, detecting a seasonal signal (frequency of 12 months) is unlikely. However, if the study period is divided into warm versus

TABLE 3

Mean (±1 SD) Ratios of Chlorophyll *a* to Ash-Free Dry Mass (AFDM) (μg mg^{-1}) Calculated from Samples Taken at the Same Site on the Same Day

	Mean	Median
AD	6.82 ± 4.02^{A}	6.14 ± 1.79
BD	4.64 ± 1.14^{B}	4.30 ± 1.21
AP	4.03 ± 1.10^{B}	3.90 ± 1.15
BP	4.98 ± 1.31^{B}	4.91 ± 1.26

Values followed by the same superscript letter are not significantly different ($\alpha = 0.05$).

TABLE 4

Chlorophyll *a* and Ash-Free Dry Mass (AFDM) (mean ± 1 SD) at the Four Sites by Season

	Winter (Nov.–Apr.)	Summer (May–Oct.)
Mean chl *a* (μg cm^{-2})		
Above-dam site	5.57 ± 4.25^{B}	6.80 ± 5.22^{B}
Below-dam site	2.44 ± 1.99^{C}	3.80 ± 4.69^{C}
Above–power plant site	4.75 ± 3.73^{B}	5.29 ± 3.44^{B}
Below–power plant site	8.85 ± 6.25^{A}	10.67 ± 6.26^{A}
AFDM mean g m^{-2}		
Above-dam site	8.13 ± 4.90^{C}	12.64 ± 9.03^{C}
Below-dam site	5.09 ± 3.49^{D}	8.91 ± 9.07^{D}
Above–power plant site	13.94 ± 21.02^{B}	13.98 ± 7.21^{B}
Below–power plant site	19.47 ± 16.75^{A}	22.80 ± 13.80^{A}

Values followed by the same superscript letter are not significantly different ($\alpha = 0.05$) for among-site comparisons.

cool months, comparisons can be made between the two times of year for the benthic pigments and organic material to test for general seasonal effects.

Comparison of chl *a* in the two seasons with repeated-measures ANOVA of natural log-transformed data showed that, in addition to the among-site differences, season also had a significant effect on benthic chl *a* ($F = 7.60$, $df = 1$, $P = 0.007$), but there was no significant site-by-season interaction ($P = 0.87$), suggesting that all four sites responded to season in a similar way. A posteriori tests indicate that the BP site had the highest chl *a* levels in both seasons and the BD site the lowest (Table 4).

An analysis of benthic AFDM, similar to that done for chl *a*, also shows, in addition to the among-site differences just discussed, strong seasonal effects ($F = 17.13$, $df = 1$, $P < 0.001$) with no site-by-season interaction ($P = 0.34$). A posteriori comparisons indicate that all four sites differed from each other in benthic AFDM over both seasons (Table 4). At the high-elevation sites there were significant differences between summer and winter months based on repeated-measures ANOVA of natural log-transformed AFDM data (AD: $F = 6.08$, $df = 1$, $P = 0.020$; BD: $F = 11.24$, $df = 1$, $P = 0.003$), but benthic AFDM did not differ between seasons at the low-elevation sites (both $P > 0.1$). Variability in median AFDM at the two high-elevation sites (AD and BD) was higher in the summer months (AD: $F = 2.95$; $df = 12, 18$; $P = 0.045$; BD: $F = 4.43$; $df = 12, 18$; $P = 0.016$). At the low-elevation sites the situation was reversed, with higher variances in the winter months, though the differences were not significant (both $P < 0.7$). There were no seasonal differences at any of the sites for the ratio of chl *a* to AFDM, suggesting that, in terms of the proportion of photosynthetic matter to total organic matter, the aufwuchs is relatively constant throughout the year at each site.

Because carotenoids can serve as protective compounds at high light levels (Hoober 1984), it was predicted that carotenoids would be higher during the summer months. This was true at all sites but only significant, as determined by a Mann-Whitney *U*-test, at the BD site ($U = 159$; $P = 0.03$; $n_1, n_2 = 12, 18$). However when carotenoids concentrations are normalized to chl *a*, there are no differences between seasons at any of the sites (all $P > 0.25$). Thus, the high summer carotenoid levels may merely reflect the generally higher amount of plant material in those months.

Cross-correlations between median chl *a* and the USGS discharge measured 0, 1,... 30 days before the pigment was sampled were generally low (Figure 10). The two sites with full flow (AD and BP) showed a negative effect of flow on chl *a* at 6–7 days before sam-

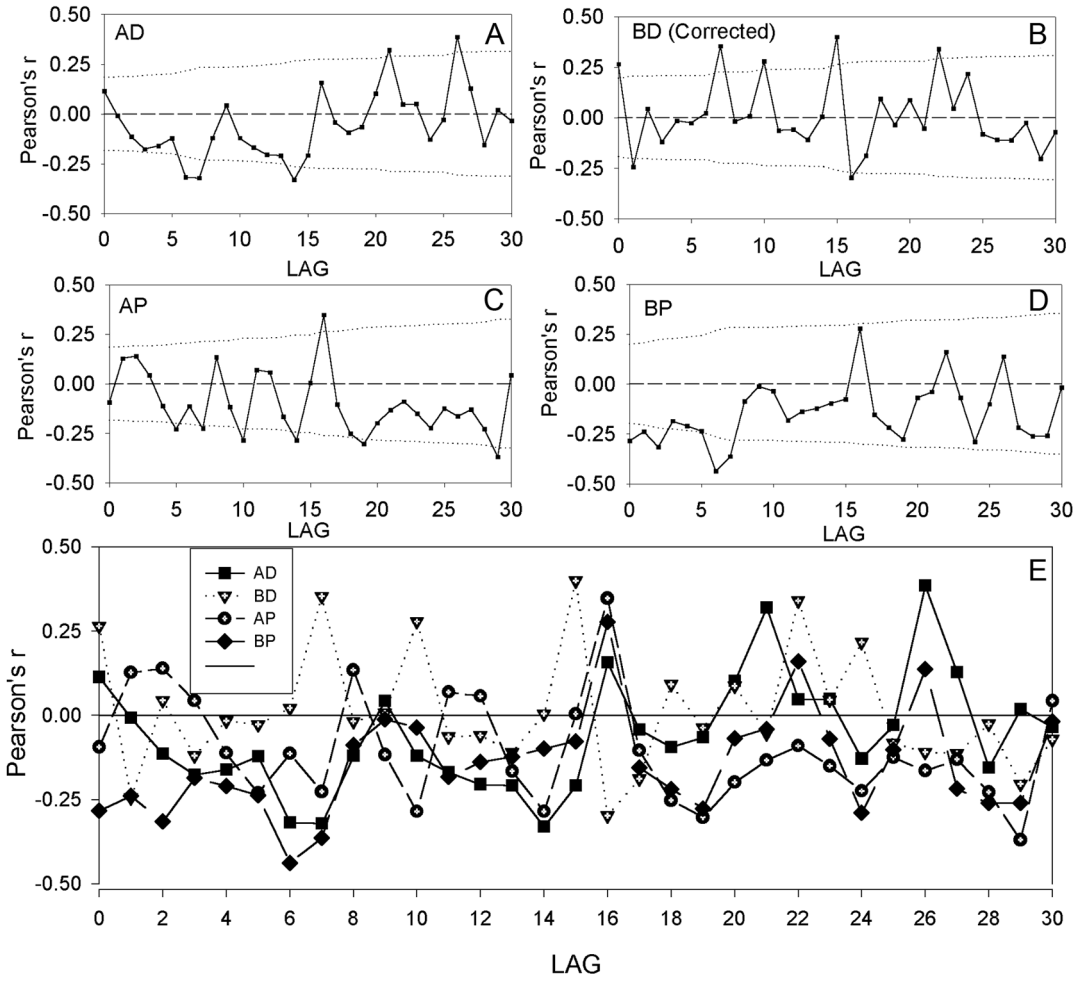

FIGURE 10. Cross-correlations (±1 standard error) between median chlorophyll *a* and the USGS discharge at 0, 1, 2,… 30 days before the chlorophyll *a* sample was taken. *A*, Above-dam site. *B*, Below-dam site. *C*, Above–power plant site. *D*, Below–power plant site. *E*, All four sites together. Solid symbols represent sites with full flow (AD and BP); open symbols represent sites with reduced flows (BD and AP).

pling (Figure 10*A* and *D*). There is some concordance among the sites, with three showing positive correlations with the flow that occurred 16 days before sampling (Figure 10*E*). The peak at the BD site appears to be offset by about 1 day relative to the other three sites.

Cross-correlations between AFDM and the USGS flow 1, 2, 3,… 30 days previously suggested a negative effect of flows 1–7 days before the benthic sampling at the two sites with full flow (Figure 11*A* and *D*). There also appeared to be some concordance (Figure 11*E*) between the two sites with reduced flow (BD and AP) for lags of 0 to about 7–8 days, but this breaks down for longer lags. All four sites exhibited concordant correlations from about day 17 to 22 and day 27 to day 30. However, when these lagged correlations were in turn correlated with each other (if they were perfectly concordant the r^2 would = 1) the only correlation greater than

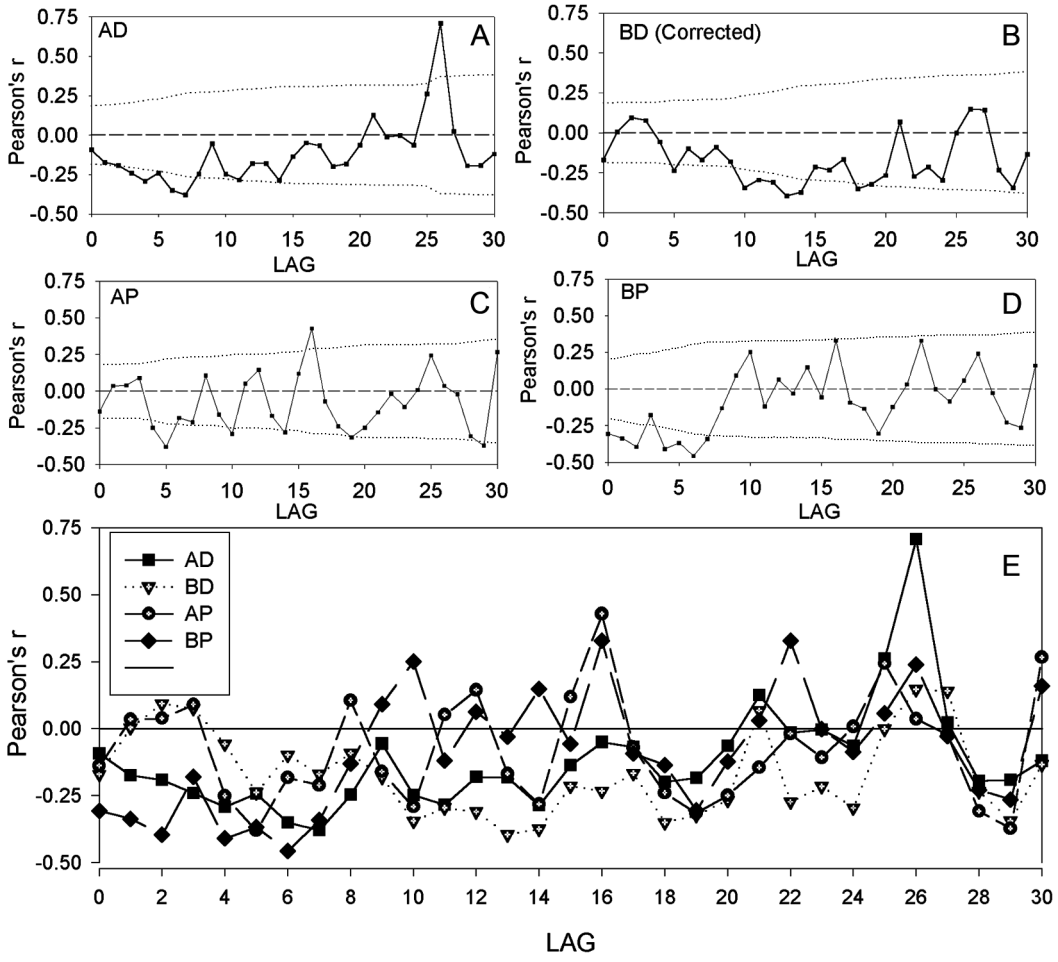

FIGURE 11. Cross-correlations (±1 standard error) between median ash-free dry mass and the USGS discharge at 0, 1, 2,… 30 days before the AFDM sample was taken. *A*, Above-dam site. *B*, Below-dam site. *C*, Above–power plant site. *D*, Below–power plant site. *E*, All four sites together. Solid symbols represent sites with full flow (AD and BP); open symbols represent sites with reduced flows (BD and AP).

0.5 was between the two sites with full flow (AD and BP).

To evaluate in-stream primary productivity we used two among-site comparisons, with tile runs carried out simultaneously at the four main-stem sites. The increase in pigment on the tiles was compared using analysis of covariance (ANCOVA) to determine if there were any differences in how quickly periphyton accumulated at the four sites. To determine if there were any differences in standing stock, the means of the final values for each run were compared. Analyses of covariance indicated that the data we collected showed no differences in either slope or magnitude among the sites in any of the six runs (all $P > 0.5$). Thus there appeared to be no marked differences in rate of accumulation of benthic algae among the sites. We also found no significant between-season differences (all $P > 0.5$). However, because many of the tiles were lost during the runs, these conclusions should be viewed with caution. A study of seasonality in benthic algal community struc-

ture in O'ahu streams also showed little evidence of seasonality (Sherwood 2004*b*).

When means of the final values were compared, the means of the two high-elevation sites (AD and BD) were always higher than those of the two lower-elevation sites (AP and BP), though many missing values precluded statistical comparison. This finding differs from the results of our monthly benthic chl *a* sampling, suggesting that the 25–40 days of growth in the tile experiments was not long enough to reach levels comparable with the standing stock of benthic chl *a*, a result also found by Wolff (2000) in this river.

Mean monthly litter fall for the five sites over the course of the study was highly variable (Figure 12). Plant input at the AD site was dominated by leaves of the introduced guava (*Psidium guajava*) and Job's tears (*Coix lacryma-jobi*). The BD site received litter from guava as well as kukui (*Aleurites moluccana*) and ginger (*Zingiber zerumbet*). Litter at the tributary site was most diverse, with māmaki (*Pipturus albidus*) and 'ie'ie (*Freycinetia arborea*) as well as guava and kukui. Litter on the left bank of the AP site consisted of mostly guava leaves and large fronds of the Alexandra palm (*Archontophoenix alexandrae*), and the right bank received mostly rose apple (*Syzygium jambos*) leaves. Hau (*Hibiscus tiliaceus*), an invasive tree that dominates low-elevation riparian zones on Kaua'i, was the dominant litter type on the left bank at the BP site, and Java plum (*Syzygium cumini*) and an unidentified bamboo species dominated the right bank. It is important to note that all litter input from riparian plants at the mainstem sites was by alien species, a situation characteristic of most low-elevation Hawaiian streams. There were significant differences among the five sites when data from all collections were pooled ($F = 9.14$, $\mathrm{df} = 4$, $P < 0.0001$). Litter fall at the high-elevation sites was generally lower than at the two low-elevation sites. The BP site received the most litter input. Variation in litter fall at the AP site was high due to the sporadic, very large inputs from the palm trees.

There was a strong seasonal component to the biomass of litter deposition (Table 5). When the samples were divided into two seasons (summer [May–October] and winter [November–April]), mean litter fall was higher at all sites in the winter months ($F = 10.06$, $\mathrm{df} = 1$, $P = 0.002$). There was no interaction between site and season ($P = 0.75$), but the among-site differences remain, suggesting that the factors that cause the sites to differ do not change through the year. Over the entire study, mean litter fall rates ranged from 1.85 g m^{-2} day^{-1} at the BD site to 2.83 g m^{-2} day^{-1} at the BP site, very similar to the rates of 1.7–2.9 g m^{-2} day^{-1} direct litter input reported by Larned (2000) for a small stream on the island of Hawai'i.

The litter we collected from the grate on the Maunahina tributary (data not shown) was dominated by guava fruit and kukui leaves. Mean biomass accumulation in the summer (344 g day^{-1} {513 g km^{-2} day^{-1}}) was greater than that in the winter months (199 g day^{-1} {297 g km^{-2} day^{-1}}), but the difference was not significant ($P = 0.3$). Larned et al. (2001) reported input of fruits (mostly guava) from upstream sources of up to 300 g day^{-1} for some months in a small Hawaiian stream, although their system and methods differed from ours. The very high variability in accumulation at the grate was probably the cause for the inability to distinguish the two seasons. September and October had very high accumulation rates, consisting mostly of guava fruits, because these months are guava fruiting season. Biomass accumulations as high as 30 kg over 6–10 days were not uncommon during these months.

In our trials, k (decomposition rate of guava leaves) ranged from −0.020 in November 1994 to −0.0057 in April 1995. There were no differences in decay rates when summer values were compared with those in the winter months ($P = 0.11$). These rates were higher than most reported from temperate streams (Rounick and Winterbourn 1983, Stewart and Davies 1989, McArthur et al. 1994, Webster et al. 1995) but similar to rates reported from tropical streams (Davies et al. 1995, Benstead 1996). The half-life of guava leaves in Wainiha may be as much as 60–70 days. This appears to be substantially longer than the 38-day half-life Archer (1983) found

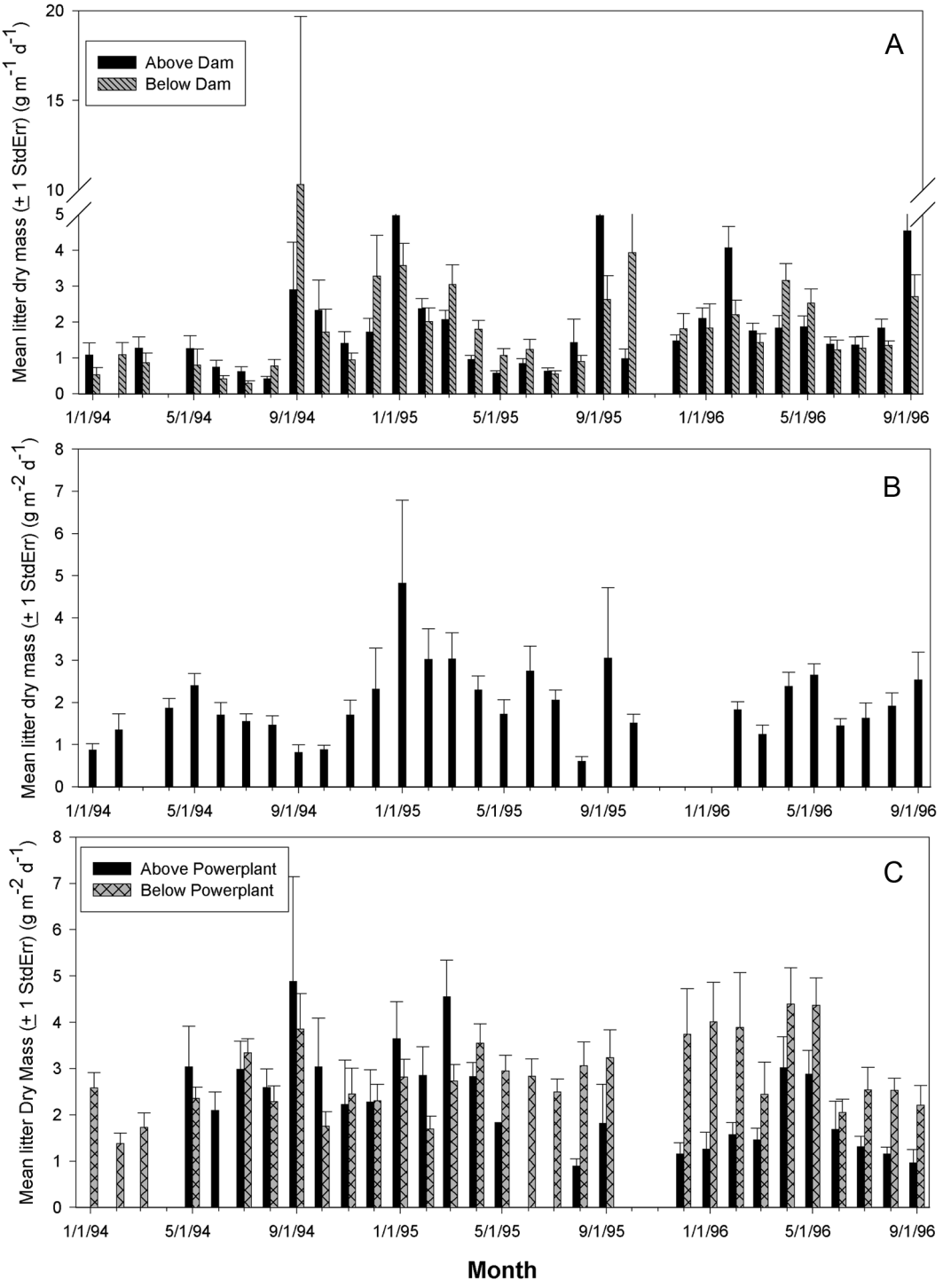

FIGURE 12. Mean leaf litter accumulation (±1 standard deviation) over the course of the study at: *A*, the AD and BD sites; *B*, the tributary site; *C*, the AP and BP sites.

TABLE 5

Leaf Litter Collected (means ± 1 SD) at the Five Study Sites

	Winter (Nov.–Apr.)	Summer (May–Oct.)
Litter (g m^{-2} day^{-1})		
Above-dam site	2.10 ± 2.50^{C}	1.87 ± 3.46^{BC}
Below-dam site	2.10 ± 2.81^{C}	1.48 ± 2.27^{C}
Tributary site	2.31 ± 2.20^{BC}	1.69 ± 1.26^{BC}
Above–power plant site	2.71 ± 3.13^{AB}	2.26 ± 4.22^{AB}
Below–power plant site	2.90 ± 2.13^{A}	2.67 ± 1.72^{A}

Values followed by the same superscript letter are not significantly different ($\alpha = 0.05$) for among-site comparisons.

for hala (*Pandanus* sp.) leaves in Waihī Stream on O'ahu. The softer leaves of hau had decay rates of −0.023 (unpubl. obs., and Larned 2000), higher than our values for guava.

Benthic Invertebrate Fauna

In terms of abundance, the benthic fauna was dominated by alien insect larvae, most notably the chironomid *Cricotopus bicinctus*. Larvae of this midge reached peak densities greater than 25 cm^{-2}. The second most abundant group at all four sites consisted of unidentified oligochaetes, probably mostly naidids. In terms of biomass, the endemic atyid shrimp *Atyoides bisulcata* dominated the biomass when it was taken. This crustacean was mostly seen at the AD site. Other than the atyid, which was taken in less than 25% of the samples, the larvae of the alien caddisfly *Cheumatopsyche analis* (previously *C. pettiti*) and the turbellarian *Dugesia* spp. were the greatest contributors to biomass at the two higher-elevation sites. *Cheumatopsyche*, *Cricotopus*, and turbellarians dominated the biomass at the two lower-elevation sites. For the analyses, we separated out life stages of some of the most common taxa because their relative sizes and ecology were different. We divided *Cricotopus* and *Cheumatopsyche* samples into larvae and pupae. *Hydroptila potosina* (previously *H. arctia*) was collected as larvae and a few pupae, but only larvae were analyzed. *Hemerodromia stellaris* was almost always taken as larvae. Atyids were divided into adults and juveniles. The remaining common taxa were lumped in higher groupings: oribatid mites, Empididae, Chironomidae (other than *Cricotopus*), and canaceids. We also lumped copepods, oligochaetes, and the remaining dipteran pupae into more inclusive groups. Like the riparian vegetation, the benthic invertebrate community in most low-elevation Hawaiian streams is dominated by alien species. Notably, Hawai'i has no native Ephemeroptera, Plecoptera, or Trichoptera.

Over the entire study period, median benthic invertebrate abundance (Figure 13*A*) showed two intervals with high numbers (December 1994 to August 1995 and April 1996 to July 1996) alternating with periods with lower abundance. There were no differences in our data for benthic invertebrates between the period when we used the Surber sampler and when we started with the Hess sampler, so results from both methods were pooled. Abundance of benthic invertebrates increased during the course of the study at all four sites (all $P < 0.04$), but, except for the BP site (regression $r^2 = 0.31$), these increases were slight, and the r^2 for the other three regressions were <0.07. There were no trends during the study period in terms of biomass of invertebrates (Figure 13*B*) except at the AD site where biomass declined ($r^2 = 0.042$, slope $= -1.45 \pm 0.60$, $P = 0.02$). From October 1995 to the end of the study there appeared to be a low and approximately equal biomass of invertebrates at all four sites (Figure 14*B*). This trend was not reflected in the data for invertebrate abundance. Atyids, which were usually only taken at the AD site, strongly influenced sample biomass. Their contribution declined from the start of the study to essentially zero after July 1995.

There were significant differences in abundance of benthic invertebrates among sites over the entire study period as determined by repeated-measures ANOVA ($F = 4.55$, df = 3, $P = 0.005$), but neither date nor the date-by-site interaction was significant ($P = 0.21$ and 0.30, respectively). A posteriori comparison of the abundances over the entire study indicates that the BP site had significantly higher abundance (mean = 8,357.5 individu-

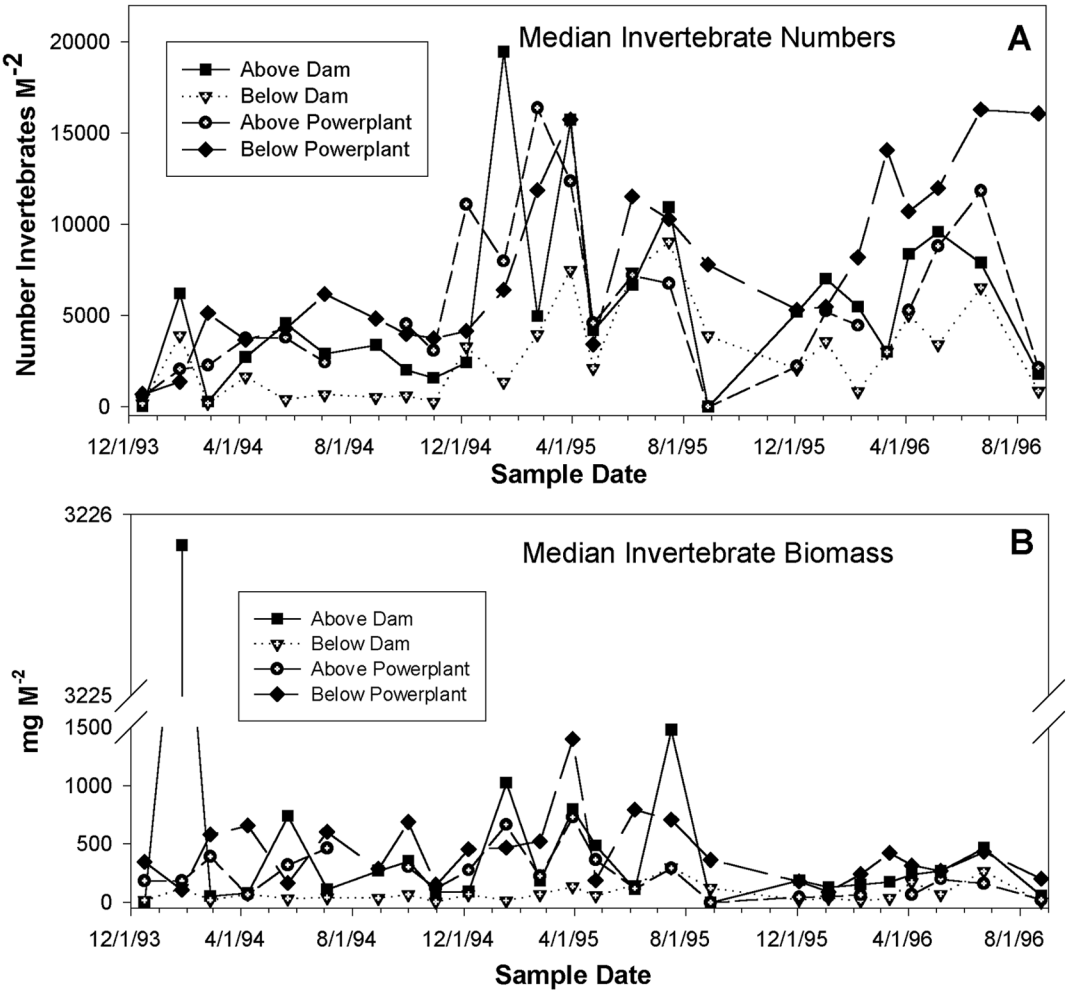

FIGURE 13. Benthic invertebrates collected during the study period at the four main-stem sites in Wainiha River. Solid symbols represent sites with full flow (AD and BP); open symbols represent sites with reduced flows (BD and AP). *A*, Median abundance. *B*, Median biomass.

als m^{-2}) than the AD and AP sites (respectively 6,738.5 and 6,675.7 individuals m^{-2}) ($P > 0.05$). The BD site had significantly fewer benthic invertebrates than the three other sites (mean = 3,211.4 individuals m^{-2}). Invertebrate densities in our study were within the range found by McIntosh et al. (2002) in a Maui stream, which like Wainiha was dominated by *Cricotopus*.

A similar analysis of biomass also indicated among-site differences ($F = 3.33$, df = 3, $P = 0.02$) with no date ($P = 0.48$) or site-by-date ($P = 0.49$) effects. A posteriori tests indicated that over the study period, the AD site had the highest benthic invertebrate biomass (mean = 1,066.3 mg m^{-1}). There was no difference between the two lower-elevation sites (AP mean = 384.9 mg m^{-1}; BP mean = 536.0 mg m^{-2}). The benthic invertebrate biomass at the BD site was significantly lower than at the other three sites (mean = 148.8 mg m^{-2}). The high biomass at the AD site was due to the fact that this was the only site where atyids were collected regularly.

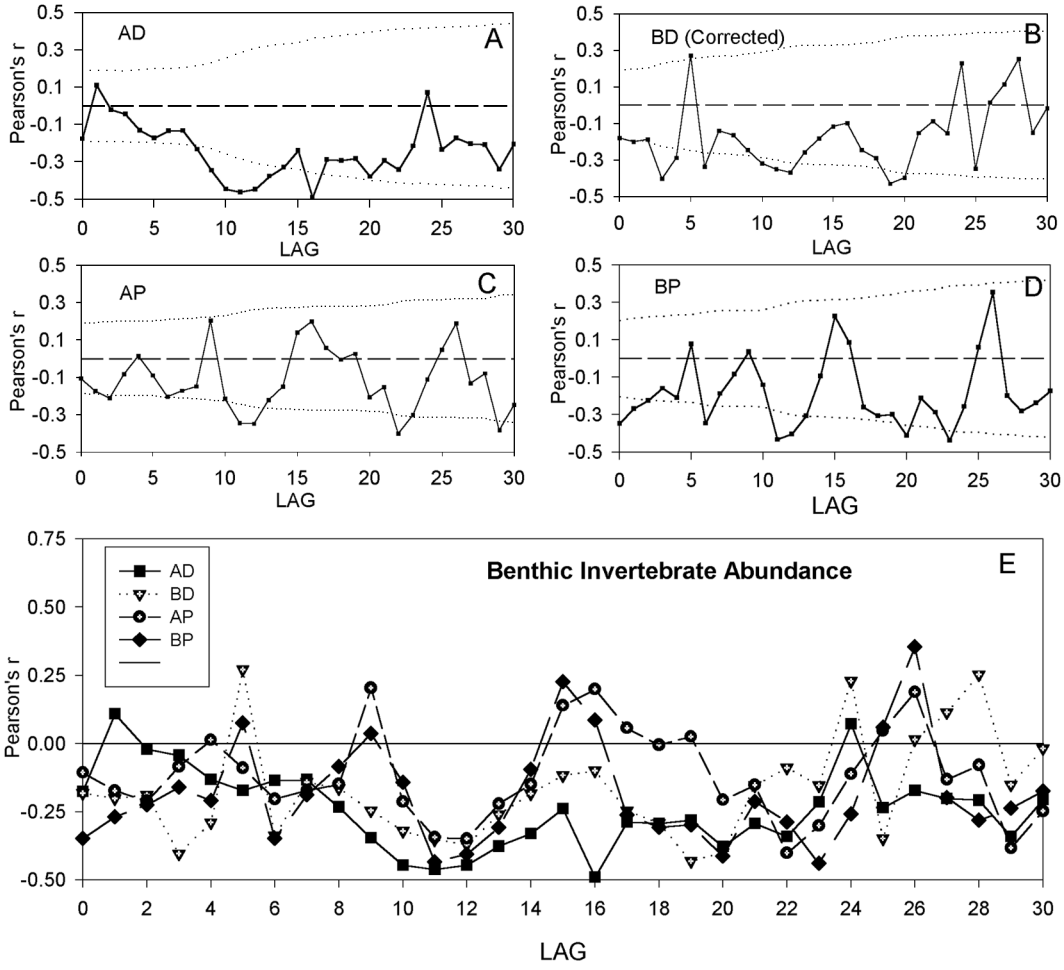

FIGURE 14. Cross-correlations (±1 standard error) between median abundance of benthic invertebrates and the USGS discharge at 0, 1, 2, … 30 days before the benthic invertebrate sample was taken. *A*, Above-dam site. *B*, Below-dam site. *C*, Above–power plant site. *D*, Below–power plant site. *E*, All four sites together. Solid symbols represent sites with full flow (AD and BP); open symbols represent sites with reduced flows (BD and AP).

When season was included as a variable (Table 6), the site effect on benthic invertebrate abundance was still strong (ANOVA on natural log-transformed abundance data: $F = 12.3$, $df = 3$, $P < 0.0001$). Season had a marginal effect ($P = 0.055$), but there was no interaction between site and season ($P = 0.61$). Abundance at the BD site was lower than at the other three sites in both seasons. When a similar analysis was run for total benthic invertebrate biomass the results were similar, with a strong site effect ($P < 0.0001$), a significant effect of season ($P = 0.002$), but no site-by-season interaction ($P = 0.96$). Biomass at the AD site was higher than at the BD site 200 m downstream in both seasons.

Cross-correlation analyses, similar to those run on the chl *a* and AFDM data, were also made for abundance and biomass of benthic invertebrates. Abundance of benthic invertebrates at the AD site showed an increasingly

TABLE 6

Benthic Invertebrate Abundance and Biomass (mean ± 1 SD) at the Four Sites by Season

	Winter (Nov.–April)	Summer (May–Oct.)
Benthic invertebrate numbers m^{-2}		
Above-dam site	$7{,}004 \pm 8{,}861^{A}$	$6{,}281 \pm 4{,}628^{B}$
Below-dam site	$3{,}158 \pm 3{,}455^{B}$	$3{,}294 \pm 3{,}553^{C}$
Above–power plant site	$6{,}790 \pm 7{,}720^{A}$	$64{,}766 \pm 5{,}664^{B}$
Below–power plant site	$7{,}657 \pm 6{,}013^{A}$	$9{,}452 \pm 6{,}019^{A}$
Benthic invertebrate biomass mg m^{-2}		
Above-dam site	$1{,}114 \pm 1{,}971^{A}$	$983 \pm 1{,}799^{A}$
Below-dam site	111 ± 164^{C}	207 ± 393^{B}
Above–power plant site	272 ± 287^{BC}	620 ± 982^{AB}
Below–power plant site	483 ± 505^{B}	619 ± 613^{AB}

Values followed by the same superscript letter are not significantly different ($\alpha = 0.05$) for among-site comparisons.

negative correlation between abundance and discharge for lags from 1 to about 10 days before the samples were taken (Figure 14*A*). Most correlation values were within 1 standard error of zero, and when they were greater, they were negative. The BD and BP sites (Figure 14*B* and *D*) showed a peak positive cross-correlation at 5 days. For lags between 10 and 15 days there was a marked among-site concordance for all four sites (Figure 14*E*), after which the two upper-elevation sites showed an increase to more positive correlations, and the two lower sites showed more negative correlations with flow.

Biomass of benthic invertebrates at the AD site showed strong positive correlation with discharge for lags of 1 to 3 days followed by a sharp drop to zero at days 4 and 5 (Figure 15*A*). The BD site showed positive correlations between benthic invertebrate biomass and flow on days 4, 5, and 10 (Figure 15*B*). Patterns at the two lower-elevation sites (Figure 15*C* and *D*) were less pronounced. Neither benthic invertebrate density nor biomass showed strong correlations with the benthic chl *a* and AFDM measured on the same sample days (all $r^2 < 0.3$).

Diversity based on abundance of benthic invertebrates was lowest at the BD site (Figure 16*A*). The period from November 1994, which began with low abundance-based diversity at all four sites that gradually increased to high levels in September 1995, overlapped the peak in total invertebrate numbers (Figure 13*A*). However, both total numbers and abundance-based diversity were high at the end of the sampling period (December 1995 to August 1996). The same upstream-downstream and seasonal trends were seen with the diversity data based on biomass (Figure 16*B*). Again the BD site was lower in diversity than the other sites.

Benthic invertebrate diversity showed a significant site effect based on repeated-measures ANOVA both for abundance and biomass (abundance: $F = 8.12$, $df = 3$, $P < 0.0001$; biomass: $F = 24.3$, $df = 3$, $P < 0.0001$). Abundance-based diversity also showed a significant date effect ($P = 0.013$), but this was not true for the biomass diversity data ($P = 0.20$). There was no interaction between site and date for either numbers or biomass diversity ($P = 0.72$ and $P = 0.96$, respectively). The BD site had the lowest diversity of benthic invertebrates both in terms of abundance and biomass, the BP site had the highest diversity, and the AD and AP sites were intermediate and did not differ from each other.

When data were divided into seasons (Table 7), there were significant site and season differences for diversity based on both abundance and biomass (all $P < 0.0001$) but no site-by-season interaction ($P = 0.71$ and $P = 0.40$ for abundance and biomass, respectively), suggesting that although the sites were very different in terms of their overall diversity, they responded to seasonal changes in a similar way.

Abundance-based diversity at the two high-elevation sites showed increasingly positive correlations with discharge from 0 to 12 days before the sample was taken (data not shown). The two lower-elevation sites both showed a strong positive peak correlation at a lag of 5 days superimposed on increasingly negative r^2 values that reached minima at day 15–16, after which the correlations became positive again. The pairs of sites at upper and lower elevations showed very similar

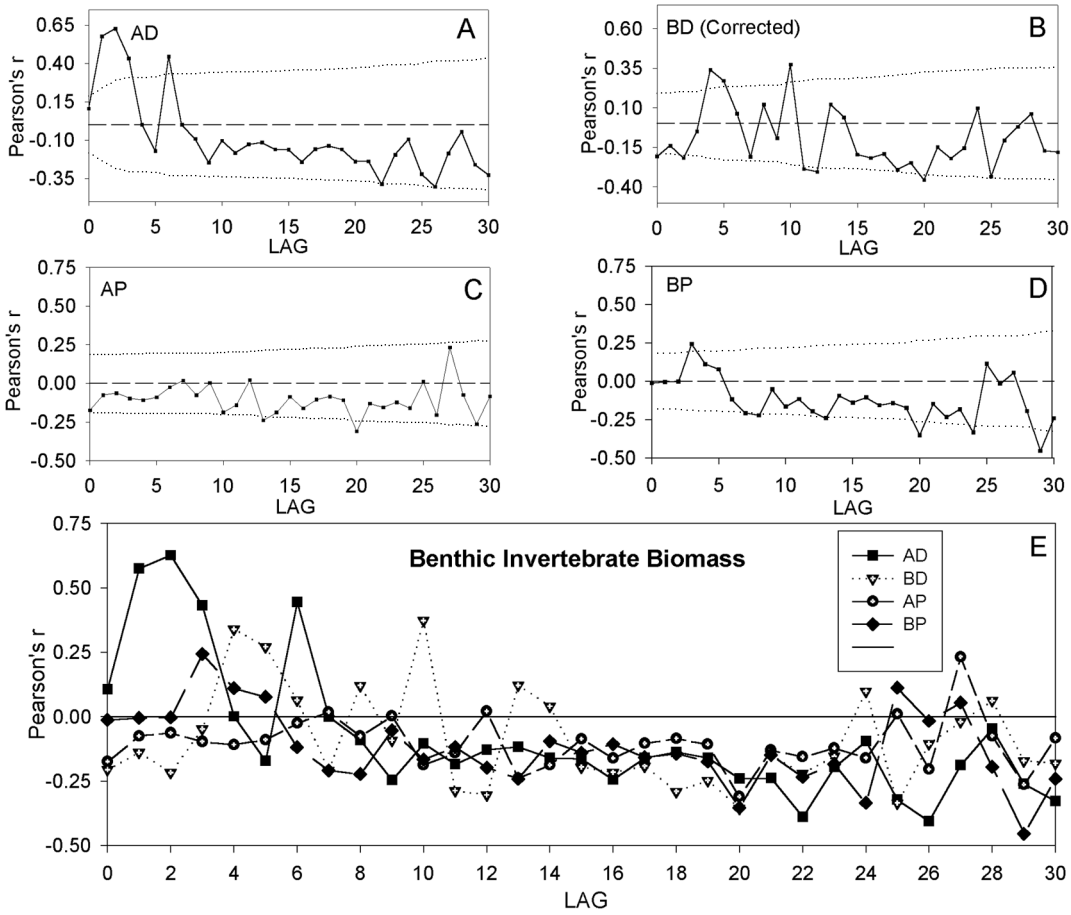

FIGURE 15. Cross-correlations (±1 standard error) between median biomass of benthic invertebrates and the USGS discharge at 0, 1, 2, . . . 30 days before the benthic invertebrate sample was taken. *A*, Above-dam site. *B*, Below-dam site. *C*, Above–power plant site. *D*, Below–power plant site. *E*, All four sites together. Solid symbols represent sites with full flow (AD and BP); open symbols represent sites with reduced flows (BD and AP).

patterns, with strong concordance for all 30 days of lagged flows.

Biomass-based diversity at the two high-elevation sites (data not shown) did not show the strong concordance that was seen in the abundance-based diversity cross-correlation analyses. For days 0 and 1 for the AD site and 0 to 5 for the BD site, correlations were strongly negative. The two lower-elevation sites showed an increasingly negative correlation between flow and biomass-based diversity for the first 4 days of lag, then a sharp peak at day 5, the same lag that showed a positive peak for abundance-based diversity.

Drift

Variability in drift at each site was high, with standard deviations often greater than the site mean. At the AP site, median abundance of drifting invertebrates showed marked peaks on a background of moderately low values (Figure 17*A*). At the two high-elevation sites, drifting biomass was sometimes strongly influenced by a single atyid in the sample (Figure 17*B*). Drifting invertebrate abundances slightly increased over the duration of the study at the AD site ($r^2 = 0.12$, slope = 0.066 ± 0.02, $P = 0.003$) but showed no trend

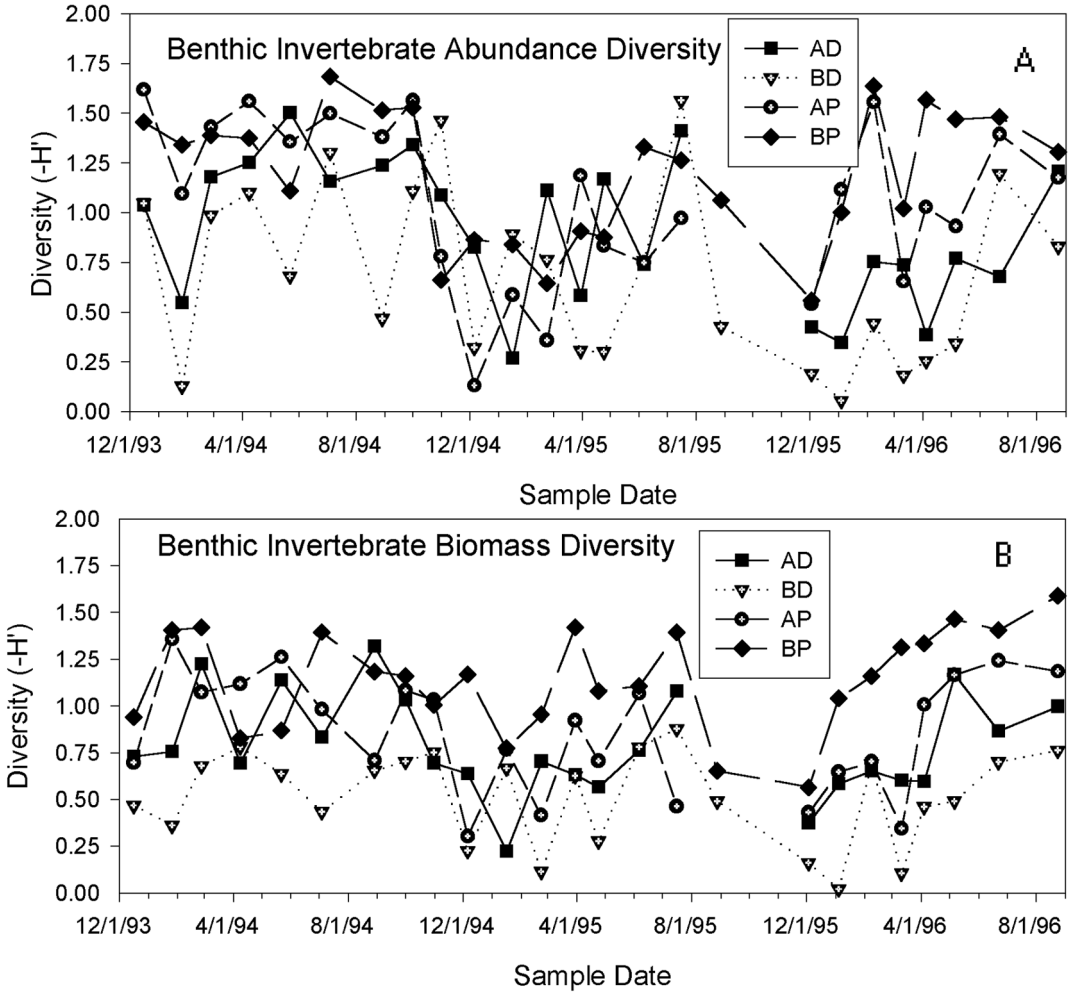

FIGURE 16. Median diversity (-*H'*) of benthic invertebrates taken at the four main-stem sites over the course of the study. Solid symbols represent sites with full flow (AD and BP), open symbols represent sites with reduced flows (BD and AP). *A*, Diversity based on abundance. *B*, Diversity based on biomass.

at the other three sites (all $P > 0.4$). In terms of biomass, there was a decline in drift at the lower-elevation sites over the study period (both $P < 0.007$), but the decrease was very slight. The two higher-elevation sites showed no significant relationship between date and drift biomass (both $P > 0.05$). There were significant differences among sites for both abundance and biomass of drifting invertebrates (repeated-measures ANOVA using natural log-transformed variables; abundance: $F = 15.8$, $\mathrm{df} = 3$, $P < 0.0001$; biomass: $F = 16.43$, $\mathrm{df} = 3$, $P < 0.0001$). There were no differences between seasons (both $P > 0.1$), nor was there any site-by-season interaction (both $P > 0.4$). Drifting invertebrates were highest at the AD site for both abundance and biomass in both seasons (Table 8).

We expected that local velocity might have an effect on drift. To test this, we regressed drift against the measured flow at each site at the time that the drift samples were being collected (i.e., directly measured flow, not USGS discharge data). At the AD site there

TABLE 7

Benthic Invertebrate Diversity (mean -H' ± 1 SD) Based on Abundance and Biomass at the Four Sites by Season

	Winter (Nov.–April)	Summer (May–Oct.)
Benthic invertebrate diversity based on total numbers		
Above-dam site	0.82 ± 0.42^{B}	1.17 ± 0.03^{A}
Below-dam site	0.59 ± 0.46^{C}	0.97 ± 0.48^{B}
Above–power plant site	0.99 ± 0.52^{A}	1.21 ± 0.39^{A}
Below–power plant site	1.14 ± 0.39^{A}	1.29 ± 0.43^{A}
Benthic invertebrate diversity based on total biomass		
Above-dam site	0.72 ± 0.46^{B}	0.91 ± 0.43^{B}
Below-dam site	0.43 ± 0.32^{C}	0.66 ± 0.35^{C}
Above–power plant site	0.83 ± 0.45^{B}	1.03 ± 0.37^{AB}
Below–power plant site	1.09 ± 0.37^{A}	1.13 ± 0.40^{A}

Values followed by the same superscript letter are not significantly different ($\alpha = 0.05$) for among-site comparisons.

was no relationship between drift and site-specific discharge for either abundance or biomass ($P = 0.17$ and $P = 0.86$, respectively). At the other three sites there were significant positive relationships between drift and water velocity, in terms of both abundance and biomass, and discharge (all $P < 0.005$). These results suggest that when drift is high it is independent of local flow, but when drift is, on average, lower it is more influenced by flow.

The AD site also showed little correlation between abundance of drifting invertebrates and the flows up to 30 days before the samples were collected (Figure 18*A*). The other three sites showed increasingly negative correlations with flow for 1–5 days previous to sampling; then a sharp change to positive correlations centered on the flow 9–11 days before sampling (Figure 18*B*, *C*, and *D*). This is consistent with our finding that the site with high drift (AD) is less influenced by flow. Correlations of drift abundance with USGS discharge at all four sites dropped sharply on days 11–13. The number of drifting invertebrates at all four sites responded to flow in similar ways (Figure 18*E*) but with fluctuations at the AD site more damped.

Patterns of cross-correlations of drifting invertebrate biomass and lagged discharge (Figure 19) are less clear than for abundance. As with abundance of drifting invertebrates, drift biomass at the AD site showed little effect of flow on days before sampling. The overall shift from positive correlations 2–3 days before sampling to generally negative correlations with flows about 15 days before sampling are clearest at the two low-elevation sites (Figure 19*C* and *D*).

Diversity of drifting invertebrates based on abundance decreased beginning in the summer of 1994 (Figure 20*A*), but the regression was only significant for the AP site ($F = 19.9$, slope $= -0.0008 \pm 0.0002$, $P < 0.001$; all others $P > 0.1$). There was a similar relationship for diversity based on biomass (Figure 20*B*), with the AP site again showing a significant but slight decline ($F = 13.9$, slope $= -0.0007 \pm 0.0002$, $P = 0.0004$) during the study. Diversity of drifting invertebrates was higher at the BP site than at the BD site for both abundance- and biomass-based diversity in winter but not summer (Table 9). For abundance-based diversity, there was a seasonal effect ($F = 12.8$, df $= 1$, $P = 0.0004$), with the warm season having higher diversity, but there was no site-by-season interaction ($P = 0.46$). For diversity based on biomass, season had no effect ($P = 0.08$). Overall, among-site differences in diversity of drifting invertebrates was less marked than for many of the other parameters we measured, suggesting stronger connectivity in drifting community composition.

When diversity of drifting invertebrates is regressed on flow measured at the site during sample collection, no sites showed any relationship for abundance (all $P > 0.05$), and only the AD site showed a significant relationship for biomass ($F = 11.7$, slope $= 0.56 \pm 0.10$, $P = 0.0011$). All sites showed a positive correlation between abundance-based diversity of drifting invertebrates and USGS discharge, though the strength of the relationship decreased downstream (AD: $r^2 = 0.11$, $P = 0.007$; BD: $r^2 = 0.08$, $P = 0.023$; AP: $r^2 = 0.08$, $P = 0.027$; BP: $r^2 = 0.05$, $P = 0.07$). Only the AP site showed a relationship between biomass-based diversity and

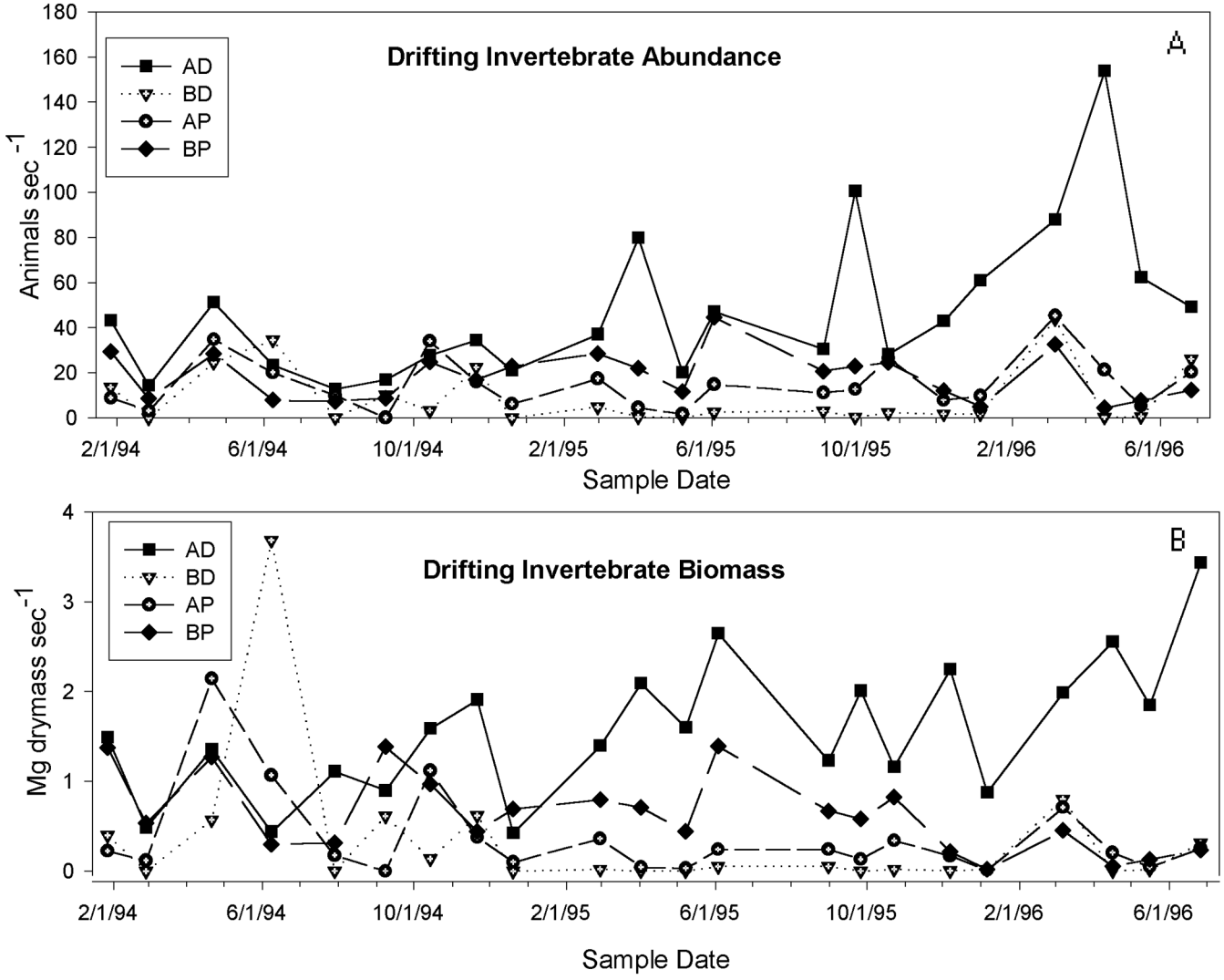

FIGURE 17. Median drifting invertebrates at the four main-stem sites in Wainiha River. Solid symbols represent sites with full flow (AD and BP); open symbols represent sites with reduced flows (BD and AP). *A*, Invertebrate abundance. *B*, Invertebrate biomass.

TABLE 8

Invertebrate Drift (mean ± 1 SD) Based on Abundance and Biomass at the Four Sites by Season

	Winter (Nov.–April)	Summer (May–Oct.)
Numbers of drifting invertebrates (no. sec^{-1})		
Above-dam site	56.46 ± 57.23^{A}	41.03 ± 29.88^{A}
Below-dam site	10.43 ± 20.17^{B}	11.99 ± 21.85^{B}
Above–power plant site	19.01 ± 18.70^{B}	13.22 ± 9.23^{B}
Below–power plant site	19.21 ± 11.24^{B}	16.82 ± 13.62^{B}
Biomass of drifting invertebrates (mg sec^{-1})		
Above-dam site	2.41 ± 4.30^{A}	2.96 ± 7.09^{A}
Below-dam site	0.20 ± 0.35^{B}	1.55 ± 3.72^{AB}
Above–power plant site	0.52 ± 0.80^{B}	0.32 ± 0.43^{B}
Below–power plant site	0.67 ± 0.51^{B}	0.58 ± 0.50^{B}

Values followed by the same superscript letter are not significantly different ($\alpha = 0.05$) for among-site comparisons.

USGS discharge ($F = 8.05$, slope $= 1.85 \pm 0.07$, $P = 0.0062$).

All four sites showed marked and increasingly negative correlation between abundance-based diversity in the drift and USGS flow for up to 9–11 days before collecting the drift sample (data not shown). After this decline, all but the AP site showed increasingly positive correlations. There was strong concordance among the other three sites for days 0–18. Diversity in the biomass of drifting invertebrates shows a pattern similar to that for abundance-based diversity (data not shown). Concordance with increasingly positive correlations with flow from 21 to 30 days before the drift sampling is marked at all four sites.

Transport of Particulate Matter

There were no differences in the ratio of CPOM:FPOM among the four sites ($F = 1.85$, df $= 3$, $P = 0.144$). However, there were differences among sites for FPOM and CPOM individually (FPOM: $F = 11.56$, df $= 3$, $P < 0.0001$; CPOM: $F = 4.97$, df $= 3$, $P = 0.003$). The BP site had higher levels of transported material in both size categories ($P < 0.05$). When transport was regressed against USGS flow on the date samples were taken the AD and AP sites showed a positive relationship between CPOM and discharge (AD: $F = 24.5$, slope $= 0.033 \pm 0.007$, $P < 0.0001$; AP: $F = 6.21$, slope $= 0.032 \pm 0.013$, $P = 0.022$), but the other two sites showed no relationship between CPOM and USGS flow on the sampling day (both $P > 0.2$). In addition, when USGS flows at 2, 5, and 10 days before the sampling date were used, there were no correlations for CPOM. There were also no relationships between FPOM or the FPOM:CPOM ratio and USGS flow on day 0, 2, 5, or 10 (all $P > 0.05$). FPOM was higher in the summer months at the AD and AP sites (AD: $F = 4.76$, df $= 1$, $P = 0.042$; AP: $F = 8.22$, df $= 1$, $P = 0.009$), but the other sites showed no relationship (both $P > 0.13$). CPOM and the FPOM:CPOM ratio showed no among-season differences at any of the sites.

DISCUSSION

Wainiha River: General Characteristics

By Hawaiian standards, Wainiha River is fairly large (third largest in the state by discharge) with a mean daily discharge of 3.9 m^3 sec^{-1}. It is typical of windward, perennial Hawaiian streams with flashy and not strongly seasonal flows. Wainiha River is functionally a very low-order stream with most surface inputs from intermittent tributaries in valley wall channels. High flows can occur in any month. The unusual trimodal annual flow pattern may be influenced by precipitation patterns in the Alaka'i wetland, because similar annual discharge relationships are also seen in neighboring streams to the west, but we could find no specific causes to explain this observation. Although discharge is not strongly seasonal, temperature, light, and many biological parameters do show seasonality. Compared with many continental streams (Allan 1995, Lewis et al. 1995), water in Wainiha is low in dissolved nutrients and salts. Dissolved silicate and total organic carbon seem most strongly influenced by discharge but in opposite ways, with silicate concentration decreasing with increased flow

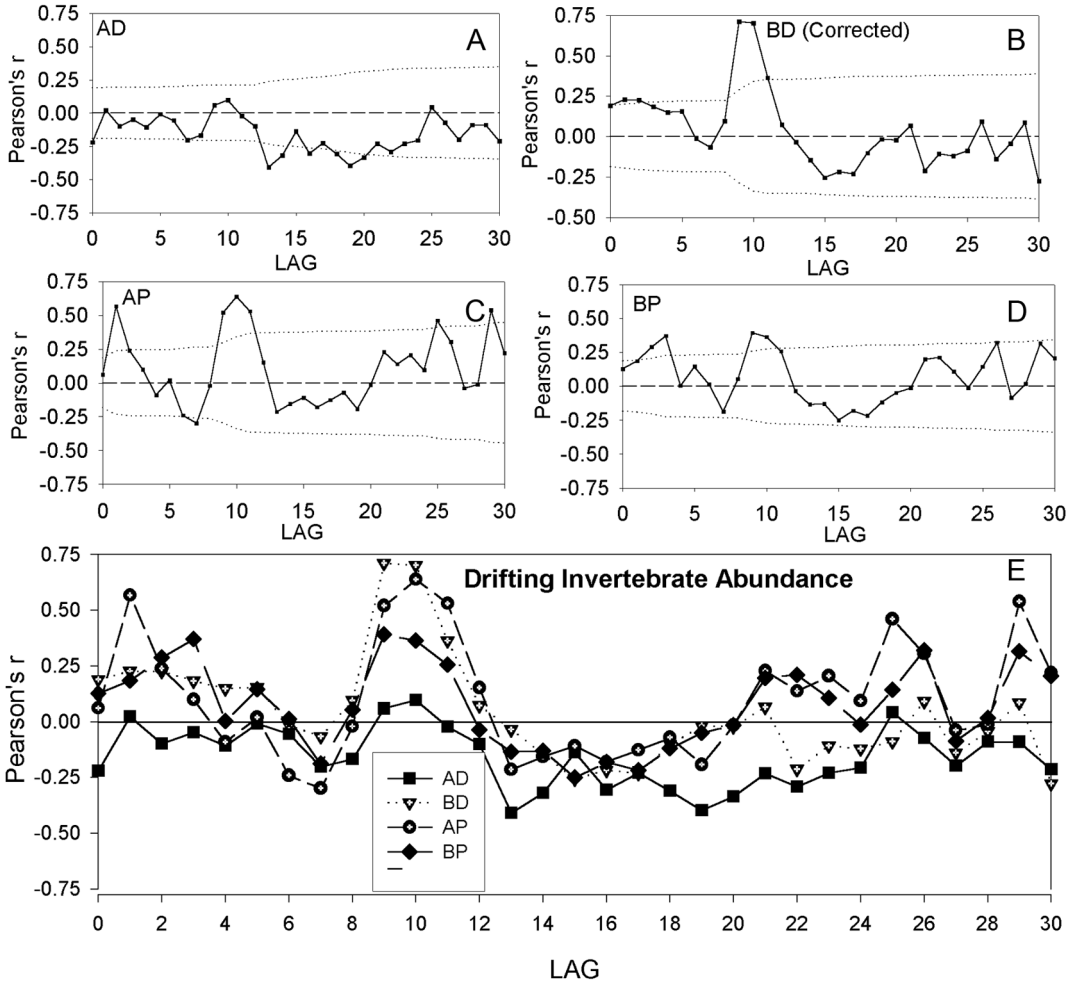

FIGURE 18. Cross-correlations (±1 standard error) between mean abundance of drifting invertebrates and the USGS discharge at 0, 1, 2,… 30 days before the drift sample was taken. *A*, Above-dam site. *B*, Below-dam site. *C*, Above–power plant site. *D*, Below–power plant site. *E*, All four sites together. Solid symbols represent sites with full flow (AD and BP); open symbols represent sites with reduced flows (BD and AP).

and total organic carbon increasing with increased flow.

Allochthonous input was dominated by leaves and, seasonally, fruits of alien plants. At the elevations where we worked there was little native Hawaiian vegetation. Allochthonous input was lower at the two upper-elevation sites than at the downstream sites. All sites showed greater leaf fall in winter months, and input of guava fruit peaked in late summer and fall. Rates of leaf breakdown in the stream did not show seasonal differences. In-stream primary production was higher at high elevations, but no seasonal differences were detected. Results of the leaf degradation studies and the in-stream primary production studies should be viewed with caution, however, because many of the trials were destroyed by high flows, resulting in less than ideal data sets.

Seasonality was marked in benthic chl *a* and AFDM, with both showing higher levels

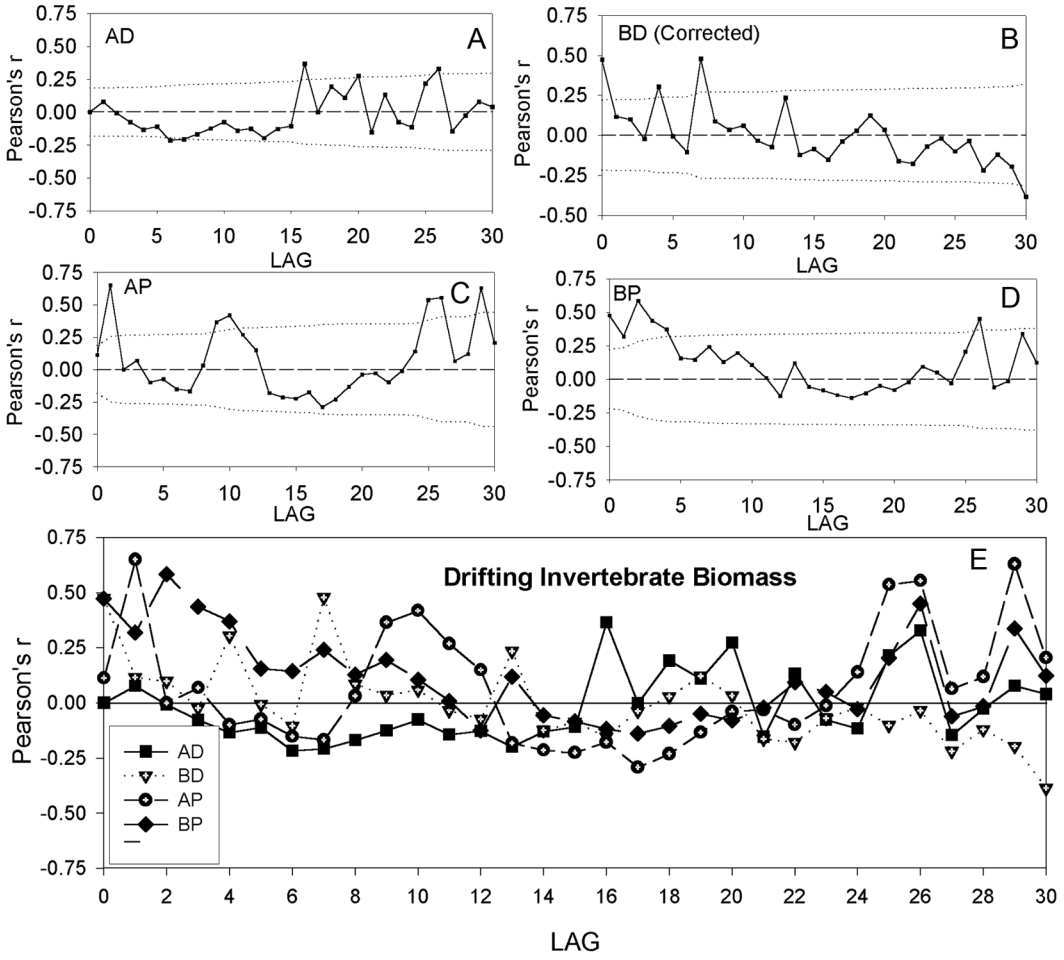

FIGURE 19. Cross-correlations (±1 standard error) between mean biomass of drifting benthic invertebrates and the USGS discharge at 0, 1, 2,… 30 days before the drift sample was taken. *A*, Above-dam site. *B*, Below-dam site. *C*, Above–power plant site. *D*, Below–power plant site. *E*, All four sites together. Solid symbols represent sites with full flow (AD and BP); open symbols represent sites with reduced flows (BD and AP).

in summer months. However, benthic invertebrates did not exhibit such strong seasonal trends either in terms of abundance or biomass. However, diversity of benthic invertebrates was higher at all sites in the warm months. This was the case whether diversity calculations were based on abundance or biomass. Drifting invertebrates showed similar patterns, with abundance and biomass showing no seasonal effect but with higher diversity in the warm months.

Abiotic Effects of the Diversion

It is not surprising that the effects of the diversion were most strongly seen at the site just below the diversion dam. Based on USGS records, on about half the days during our study the dam diverted all the water, resulting in no flow in the main channel immediately below the dam. Only leakage and seeps fed the stream on these occasions. Averaged over the entire study, discharge at the below-

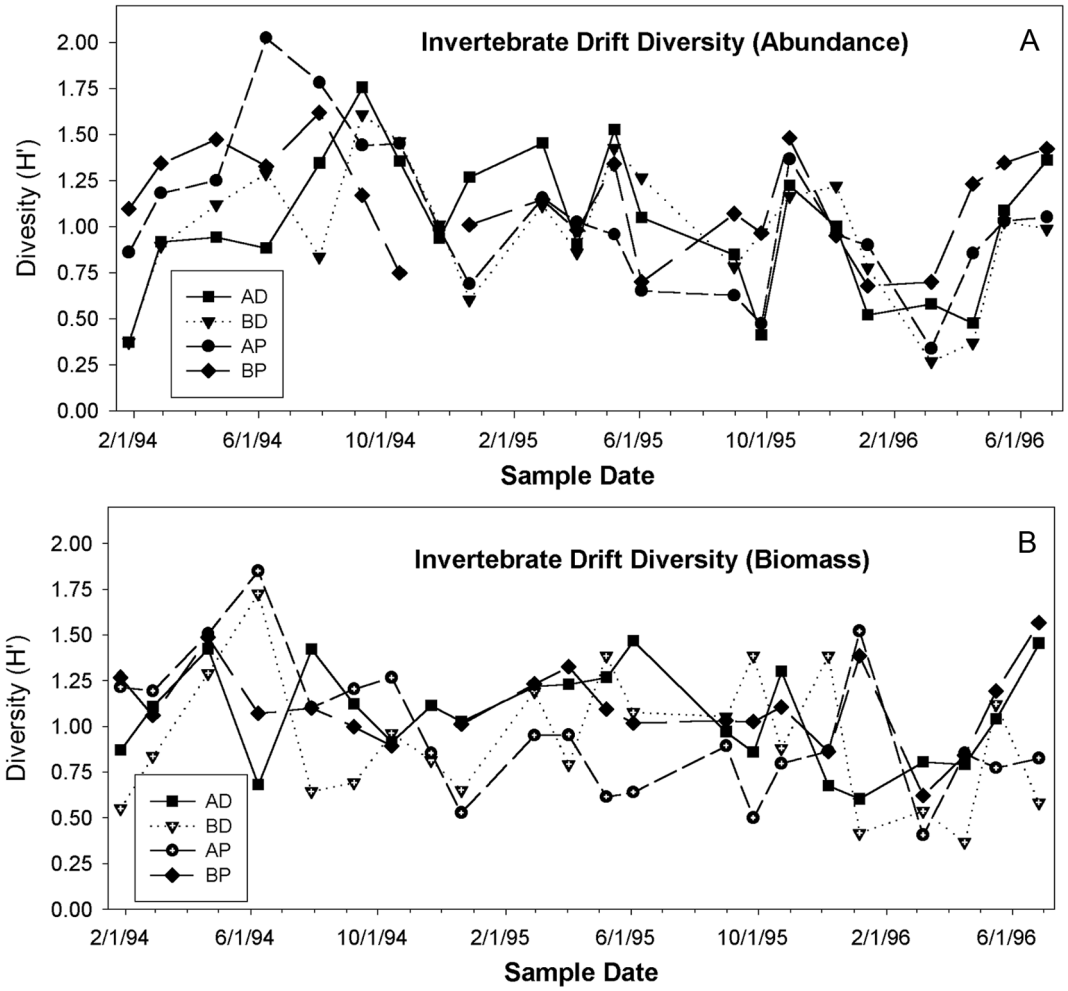

FIGURE 20. Diversity (*H′*) of drifting invertebrates in Wainiha Stream. Solid symbols represent sites with full flow (AD and BP); open symbols represent sites with reduced flows (BD and AP). *A*, Diversity based on abundance. *B*, Diversity based on biomass.

dam site was 17% of that at the site just 200 m upstream. Even though flow was so strongly reduced at the BD site, mean temperatures there were not different from those at the AD site, probably because extensive leakage through and under the dam and side-stream groundwater inputs kept temperatures low. Unlike temperature, conductivity at the BD site was strongly influenced by the diversion.

Even though it was more than 6 km downstream from the dam, the AP site also showed influences of the diversion. In gaining streams such as Wainiha, a site so far downstream would be expected to have substantially greater flow than an upstream site, but this was not the case in Wainiha. Discharge at the AP site was only 60% of that of the undiverted flow at the AD site. Periodic floods have kept the channel open, with vegetation set back from the stream margins. The valley floor near the AP site is broad so that floods extend the width of the channel rather than

TABLE 9

Average Diversity (-H' mean ± 1 SD) of Invertebrate Drift Based on Abundance and Biomass at the Four Sites by Season

	Winter (Nov.–April)	Summer (May–Oct.)
Diversity of drifting invertebrates based on numbers (-H')		
Above-dam site	0.97 ± 0.39^{AB}	1.14 ± 0.37^{A}
Below-dam site	0.86 ± 0.37^{B}	1.11 ± 0.32^{A}
Above–power plant site	0.99 ± 0.29^{AB}	1.19 ± 0.52^{A}
Below–power plant site	1.11 ± 0.30^{A}	1.15 ± 0.31^{A}
Diversity of drifting invertebrates based on biomass (-H')		
Above-dam site	0.10 ± 0.38^{AB}	1.09 ± 0.38^{A}
Below-dam site	0.85 ± 0.43^{B}	1.03 ± 0.50^{A}
Above–power plant site	0.92 ± 0.39^{AB}	1.01 ± 0.51^{A}
Below–power plant site	1.08 ± 0.37^{A}	1.08 ± 0.33^{A}

Values followed by the same superscript letter are not significantly different ($\alpha = 0.05$) for among-site comparisons.

cutting deeper. The wetted channel at this site usually only occupied about 30% of the total streambed, resulting in shallow, high-light conditions. This in turn produced mean temperatures and daily temperature excursions that were the highest in our study. Conductivity was highest at the AP site, but phosphate, nitrate, and total dissolved phosphorus were low there. Because of these interacting factors, the anomalous biotic parameters we observed at the AP site could not simply be assigned to effects of reduced flow per se. Instead, the effects of the diversion acted on several different processes and at different temporal and spatial scales.

The BP site was also influenced by the diversion, not by water removal but by the return of water that had flowed through the flume system and was returned to the main channel at the power plant. We did not measure velocity of water flowing in the flume relative to flow in the main channel, but it is likely that the travel time from the dam to the power plant was less in the relatively straight and smooth flume system. Discharge at the BP site was about 110% of that at the AD site above the diversion, lower than expected for a gaining stream such as Wainiha. However, below the power plant the stream splits into two channels so that the total flow across the entire stream was closer to 175% of that at the AD site. Water at the BP site was a mixture of water that had remained in or accumulated in the main channel and water that was delivered by the diversion system. Although mean temperatures at the BP site were warmer than at the higher elevations, they were below those at the AP site. Conductivity at the BP site reflected a simple mixing of the two sources.

Biotic Effects of the Diversion

As with physical parameters, the biotic effects of the diversion were most strongly marked at the BD site, mixed at the AP site, and the BP site exhibited complex responses. The BD site had the lowest benthic plant pigments and benthic organic matter, as well as numbers, biomass, and diversity of benthic and drifting invertebrates. The effects of the diversion immediately upstream of this site were significant in all cases.

Conditions at the AP site were mixed. Upstream/downstream gradients predicted by the river continuum concept, as well as many empirical studies, suggest that in unaltered streams most of the biotic parameters we measured should have been higher at the low-elevation sites (Cummins 1974, Vanotte et al. 1980, Allan 1995). However, we found that there was no difference in benthic chl *a* between the AD and AP sites, though AFDM was higher at the low-elevation site. Contrary to predictions from the river continuum concept, productivity was generally lower at the AP site than at the high-elevation sites, perhaps influenced by the reduced flow, marked temperature fluctuations, and lower than expected nutrient levels. Also contrary to what would be expected in undiverted streams, the AP site did not differ from the AD site in terms of abundance of benthic invertebrates and was actually lower in benthic invertebrate biomass.

Because so little is known about invertebrate species diversity in tropical streams

(McIntosh et al. 2002, Smith et al. 2003), and because in Hawai'i alien species now typically dominate community structure, we had no a priori ideas about upstream/downstream trends in invertebrate species diversity. We found that diversity of benthic invertebrates at the AP site did not differ from that at the high-elevation AD site. Diversity in abundance of drifting invertebrates at the AP site was lower than at the AD site, and in terms of diversity of biomass of drifting invertebrates the AP site was lower than both the AD and BP sites. Because primary productivity, benthic and drifting biomass, and diversity of invertebrates in undiverted streams might be expected to increase downstream, the low levels for some of these parameters at the AP site might have been a function of the reduced flow, directly or indirectly (e.g., the harsher temperature regime at this site).

A noteworthy feature of the benthic invertebrate community was the high density and biomass of the turbellarian flatworm. We have noted similar densities in streams on O'ahu and Hawai'i. The effect that these consumers have on the function of stream ecosystems is likely to be important because of their high numbers yet is entirely unstudied in Hawai'i.

Another impact of the diversion system was the mixing of the two water bodies at the tailrace of the power plant. The injection of "high elevation" water to this low-elevation site was evident in the physical and chemical characteristics of the water at the BP site. In years with very high temperatures this addition of cooler water at the low elevation could lower stream temperatures at lower elevations. It might be expected that water passing through the power plant would be depleted of (intact) drifting invertebrates. If this were true, drift measures should be low at the BP site. The data did not support this prediction. All measures of the drift at the BP site were equal or higher than those at the AP site.

Effects of Recent Flow Events on Biotic Parameters

Our third goal was to determine whether effects of flow on the instream biotic parameters we measured were detectable after a period of a few days to weeks. Our intent was not to document changes following very high flow events (Fitzsimons and Nishimoto 1993) but rather to analyze responses to more frequent fluctuations in flow (Imbert and Perry 2000, Biggs and Smith 2002).

We approached this question using cross-correlation analyses. Interpretation of these results should be approached with caution. In all there were more than 1,300 correlation coefficients calculated. Moreover all were highly correlated because each Pearson's r was based on the same USGS discharge data set and the same biotic parameter was used 30 times, once for each lag. Given these concerns about the cross-correlation analysis approach, the statistical problems inherent in such methodology (Olden and Neff 2001), and the blurring of environmental effects because of the sampling scheme, the fact that the approach did give some insights into the patterns of parameter responses was, perhaps, surprising. A more directed sampling system where samples are taken after several high flow events (Jenkins and Boulton 2003) or during prolonged droughts (Larned 2000) would improve the ability to detect responses in a more efficient manner.

Both benthic chl *a* and AFDM showed a similar pattern in their cross-correlations with flow. At all four sites, the parameters showed negative correlations with flows that occurred 5–8 days before the sample was taken. This suggests that a recovery period of about 5 days may be required for the aufwuchs to readjust to flow disturbances. The abundance and biomass of benthic invertebrates at the AD site showed a similar relationship with flows preceding collection, but the recovery time may have been closer to 10 days. This pattern was not seen at the other three sites. The concordance in cross-correlation values for both benthic invertebrate numbers and biomass at lags from about 8 to 22 days was strikingly similar at all four sites.

Over the course of the study, number of benthic invertebrates and diversity of benthic invertebrates based on numbers exhibited a more or less reciprocal pattern. Given this observation it is not surprising that while

the cross-correlations with abundance became more negative with increased lags, abundance-based diversity showed the opposite trend at the AD site. Diversity based on abundances showed clear high-elevation versus low-elevation differences. Biomass-based diversity showed no such patterns.

The data did not show the increase in the proportion of fine suspended matter predicted by the river continuum concept. However, Wainiha is different in many ways from the large temperate stream systems that formed the basis of the river continuum concept. The concept was developed to predict changes from small headwater streams with complete canopy cover through high-order floodplain rivers. Wainiha functions as a very low-order stream, and we only sampled in the middle and lower reaches. Small headwaters of streams such as Wainiha are located high up the almost vertical valley walls and so are almost totally unstudied. Another major difference in Hawaiian streams is the lack of many insect orders that play important roles in continental streams (Larned et al. 2003). Their absence, particularly large active shredders, may result in very different community processes (Chong et al. 2000).

Dewaterment in this stream ecosystem had not only the expected effects of reduction of available habitats in reaches with low flow but also many complex and sometimes subtle impacts that even our detailed investigation could merely point out, not explain. Because stream alteration, in Hawai'i and elsewhere, is certainly going to continue in the future, it is important to understand not only the direct effects of dewaterment but also the indirect ones. To do this we must first learn much more about how intact systems function and the impacts of the domination of stream and riparian habitats by alien species.

CONCLUSIONS

One of the major questions at the outset of the study concerned the effects of the hydropower diversion system in Wainiha River on abiotic and biotic parameters. Near the diversion the effect was dramatic. There was no flow over the dam at least half the time during our study. On those days the only water in the channel at the site immediately below the dam (BD) was from springs and seeps. Downstream, discharge at the site just before the diverted water was returned (AP) was, on average, 53% of the discharge at the site where the water was replaced in the stream (BP). Monthly mean temperatures at the AP site were 1.7 °C higher than at the BP site, as were the daily temperature ranges. Conductivity at the AP site was also higher and more variable than at the BP site just downstream.

We found that benthic parameters in the reaches with reduced flow due to the diversion also showed responses attributable to the low flow conditions. Benthic chlorophyll *a* was lowest at the site with most reduced flow (BD) but showed no difference between the highest site (AD) and the AP site just above the power plant. The BP site had the highest benthic chl *a*. This relationship holds whether the entire data set is pooled or when the two seasons are treated separately. Ash-free dry mass was also lowest at the site just below the dam. Except for that site, there was a general increase in benthic AFDM downstream, although AFDM at the AP site was only 70% of that at the BP site just downstream. Taken together these data indicate the very strong negative effect of the diversion dam at the site immediately below it, and a smaller but still clear reduction in benthic pigments and AFDM at the low-elevation site with reduced flow. Benthic invertebrates were reduced just below the diversion dam in terms of abundance, biomass, and diversity. Abundance and diversity of benthic invertebrates was highest at the low-elevation site with restored flow (BP), and biomass was highest at the high-elevation site with full flow (AD) mainly because the large atyid shrimps were generally found only above the dam.

Downstream invertebrate drift was also influenced by reduced flows. Abundance of drifting invertebrates was lowest at the BD site but highest at the AD site just 200 m upstream. This suggests that most of the drifting invertebrates were entrained into the

diversion ditch. Biomass of drifting invertebrates shows the same trend. The BP site had higher biomass than the AP site just upstream, suggesting that some drifting invertebrates make it through the power plant intact. Although reduced flows appeared to reduce abundance of drift, the diversity of drifting invertebrates did not differ among sites.

Our second research question related to the effects of changing flow on the parameters we studied. We addressed this aspect using time series cross-correlation analyses. The power of these tests was weak because of constraints on the data. However some trends were suggested. Chlorophyll *a* showed positive correlations with discharge 15–16 days previously at all four sites, and AFDM showed a similar peak at 16 days but only at the two lower-elevation sites. All but the BD site showed negative correlations with the discharge that occurred 4–6 days previously for both chlorophyll *a* and AFDM. At the AD site, biomass of benthic invertebrates showed positive correlations with discharge 1–3 days before. There was little evidence of such a relationship for biomass at the other three sites, and benthic abundance showed no relationships at any of the sites. Diversity of benthic invertebrates based on abundance showed similar cross correlation patterns at the two upper sites and at the two lower sites, but there was little similarity between the two pairs. Diversity based on biomass showed no such trends. Drifting invertebrate abundance showed concordant patterns at all four sites, with positive correlations with discharge 9–10 days previously, followed by a decrease to negative correlations. Relationships between biomass of drift and discharge were generally weak except for positive correlations at the BP site for flows 1–4 days earlier. Diversity of drifting invertebrates at all four sites, whether based on abundance or biomass, showed similar patterns of increasingly negative correlations for days 1–12.

These complex responses mean that to understand structure and functioning of Hawaiian stream systems, hydrology and biology must be studied together, and that sampling scales must include adequate spatial and temporal coverage.

ACKNOWLEDGMENTS

Thanks are due to McBryde Sugar Company and its successors for permission to access Wainiha River. We appreciate the support of the people of the Hanalei and Wainiha communities. The manuscript was improved by careful reading and comments by F. Cox, J. Ford, and three anonymous reviewers.

Charles T. "Charlie" Chong, 1962–2005

Authors Devrell, Lindstrom, Kinzie, and Wolff dedicate this paper, the results of our joint effort, to the memory of Charlie Chong, who died just as the manuscript moved to publication. Charlie's energy, dedication, and love for Hawaiian streams were the foundation on which this study rests and the spirit that guided it to completion. We, and all who care for these Islands, will miss him. Aloha.

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